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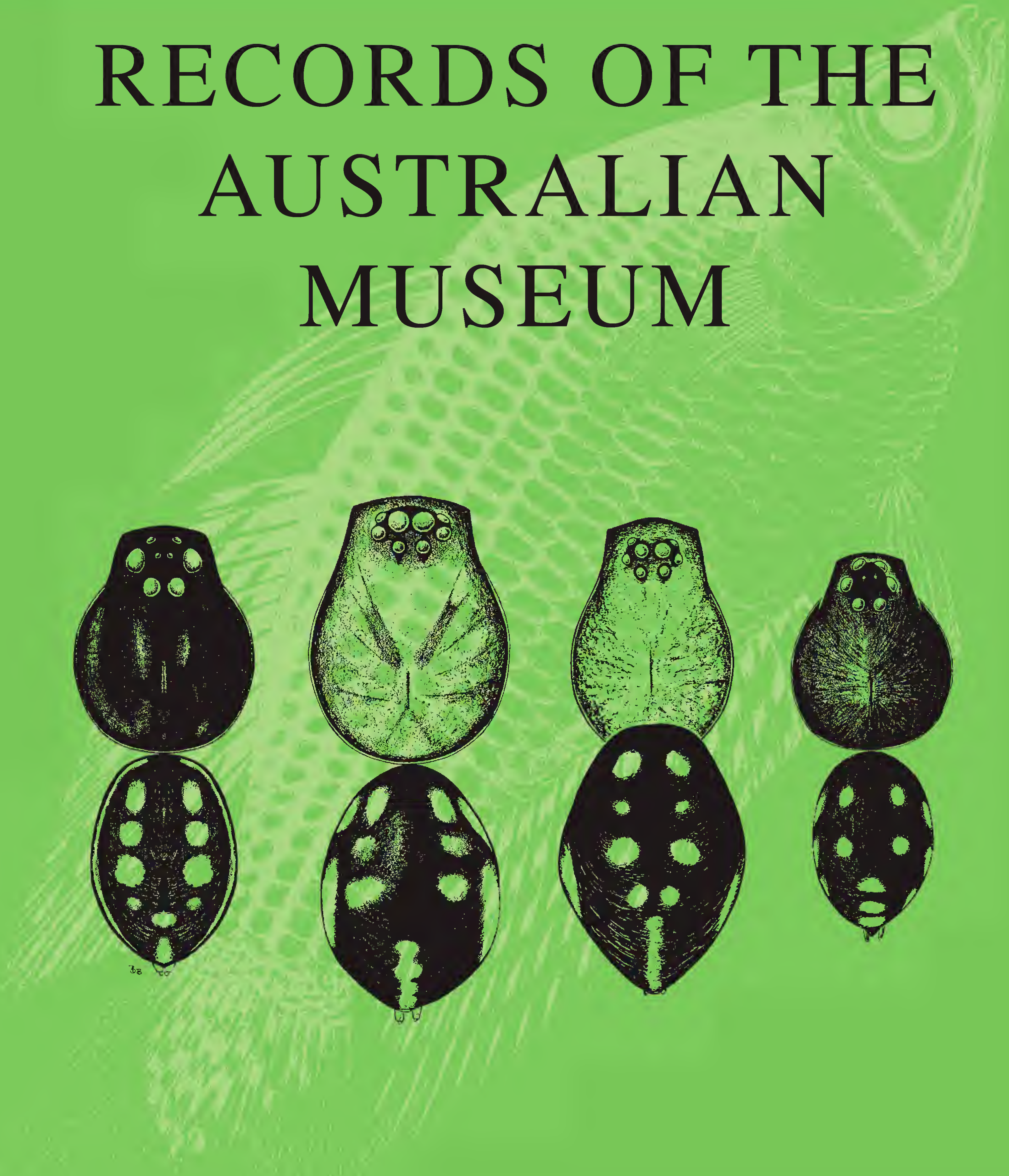
RECORDS OF THE AUSTRALIAN MUSEUM



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RECORDS OF THE AUSTRALIAN MUSEUM

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The **cover** images are of the bodies of four spider species new to science: *Habronestes pseudoaustraliensis, H. rawlinsonae, H. hebronae* and *H. monocornis* discovered in New South Wales and described and illustrated by Barbara Baehr in *Records of the Australian Museum* last year.* The faded impression of a central Queensland freshwater fish originally named *Aidapora carteri* by Australian Museum ichthyologist Gilbert Whitley provides background. This species was also first reported in *Records of the Australian Museum* volume 29 (1935).

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Two New Species of the Henicopid Centipede *Henicops* (Chilopoda: Lithobiomorpha) from Queensland and Victoria, With Revision of Species from Western Australia and a Synoptic Classification of Henicopidae

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ABSTRACT. *Henicops* Newport, 1844, is the most commonly recorded Australian genus of Henicopidae, the main southern temperate clade in Lithobiomorpha. *Henicops* is widespread throughout eastern and southwestern Australia and New Zealand, and is represented in New Caledonia by *H. brevilabiatus* (Ribaut, 1923) n.comb. New species are *H. tropicanus* n.sp. from northeastern Queensland and *H. milledgei* n.sp. from Victoria. The two nominal species from the southwest of Western Australia, *H. dentatus* Pocock, 1901a, and *H. oligotarsus* Attems, 1911, are synonymous, this species being distinguished from the Queensland *H. tropicanus* by details of the mandibular gnathal edge and female gonopod. Other characters used for diagnosing species and supraspecific groups within *Henicops* include the segmentation of the tarsi, tergite shape, and the position of the Tömösváry organ. All species of Henicopidae are listed with synonymies, generic assignments and geographic occurrences.

HOLLINGTON, LAUREN M., & GREGORY D. EDGECOMBE, 2004. Two new species of the henicopid centipede *Henicops* (Chilopoda: Lithobiomorpha) from Queensland and Victoria, with revision of species from Western Australia and a synoptic classification of Henicopidae. *Records of the Australian Museum* 56(1): 1–28.

The lithobiomorph genus *Henicops* Newport, 1844, is one of Australia's most commonly found centipede taxa, with abundant records through all eastern states and southwestern Western Australia, as well as a broad distribution in New Zealand. Despite its abundance, systematic work on *Henicops* has been limited to brief descriptions of four named species.

Excluding those species that were transferred to *Lamyctes* Meinert, 1868, after that genus was established, the nominal species of *Henicops* are the type, *H. maculatus* Newport, 1844, *H. impressus* Hutton, 1877, *H. dentatus* Pocock, 1901a, and *H. oligotarsus* Attems, 1911. *Henicops maculatus* was established for Tasmanian material, and the species has also been recorded from New Zealand, Victoria and New South Wales (Pocock, 1901a; Chamberlin, 1920; Archey, 1917, 1937). *Henicops impressus*, described from Dunedin and Queenstown, New Zealand, is considered a synonym of *H. maculatus*, which is widespread and common in New Zealand (Archey, 1937). *Henicops dentatus* was erected for specimens from Perth, Western Australia, and *H. oligotarsus* from various sites in southwestern Western Australia. The possible synonymy of these Western Australian species was suggested by Archey (1937: 75). The most recent taxonomic work on *Henicops* is Archey's

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(1937) description of New Zealand material of *H. maculatus*, with a subsequent summary of that species' distribution in Tasmania (Mesibov, 1986).

The existing literature pre-dates most collections in Australian museums. These collections indicate that the distribution of *Henicops* is more extensive than previously recorded, notably ranging to the Cape York Peninsula in Queensland (Fig. 1). The present study is based on a survey of *Henicops* samples in the collections of state museums in Australia and the Australian National Insect Collection. The overwhelming majority of specimens were collected in wet sclerophyll forest and rainforest during litter invertebrate surveys, primarily since the 1970s. This study documents two new species from Queensland and Victoria, and revises Western Australian species that are considered to be closely allied to the Queensland species. To summarize the current state of henicopid taxonomy, the new species and all confamilials are placed in a synoptic classification of Henicopidae.

Methods and terminology

Scanning electron micrographs were captured using a LEO 435VP, most using a Robinson backscatter collector.

In all species descriptions, length of specimens was measured from the anterior margin of the head shield to the end of the telson. Because this measure is affected by telescoping, length or width of the head shield is used as a measure of body size (Andersson, 1978). Terminology used throughout species descriptions follows that used by Edgecombe (2001), with terminology pertaining to the mandible following Edgecombe *et al.* (2002). For new species, "Other material" is not part of the type series.

The following abbreviations are used for repositories of the specimens examined:

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, Canberra
CAS	California Academy of Sciences, San Francisco
MV	Museum Victoria, Melbourne
NMW	Naturhistorisches Museum, Wien
QM	Queensland Museum, Brisbane
WAM	Western Australian Museum, Perth
ZIUH	Zoologisches Institut und Zoologisches Museum der Universität Hamburg

Abbreviations for collectors are: GBM, G.B. Monteith; JMW, J.M. Waldock; MSH, M.S. Harvey; RWT, R.W. Taylor. Other abbreviations for label data are: ANZSES, Australian and New Zealand Scientific Exploration Society; Berl., ANIC Berlesate sample; NP, National Park; Ra, Range; rf, rainforest; SF, State Forest.

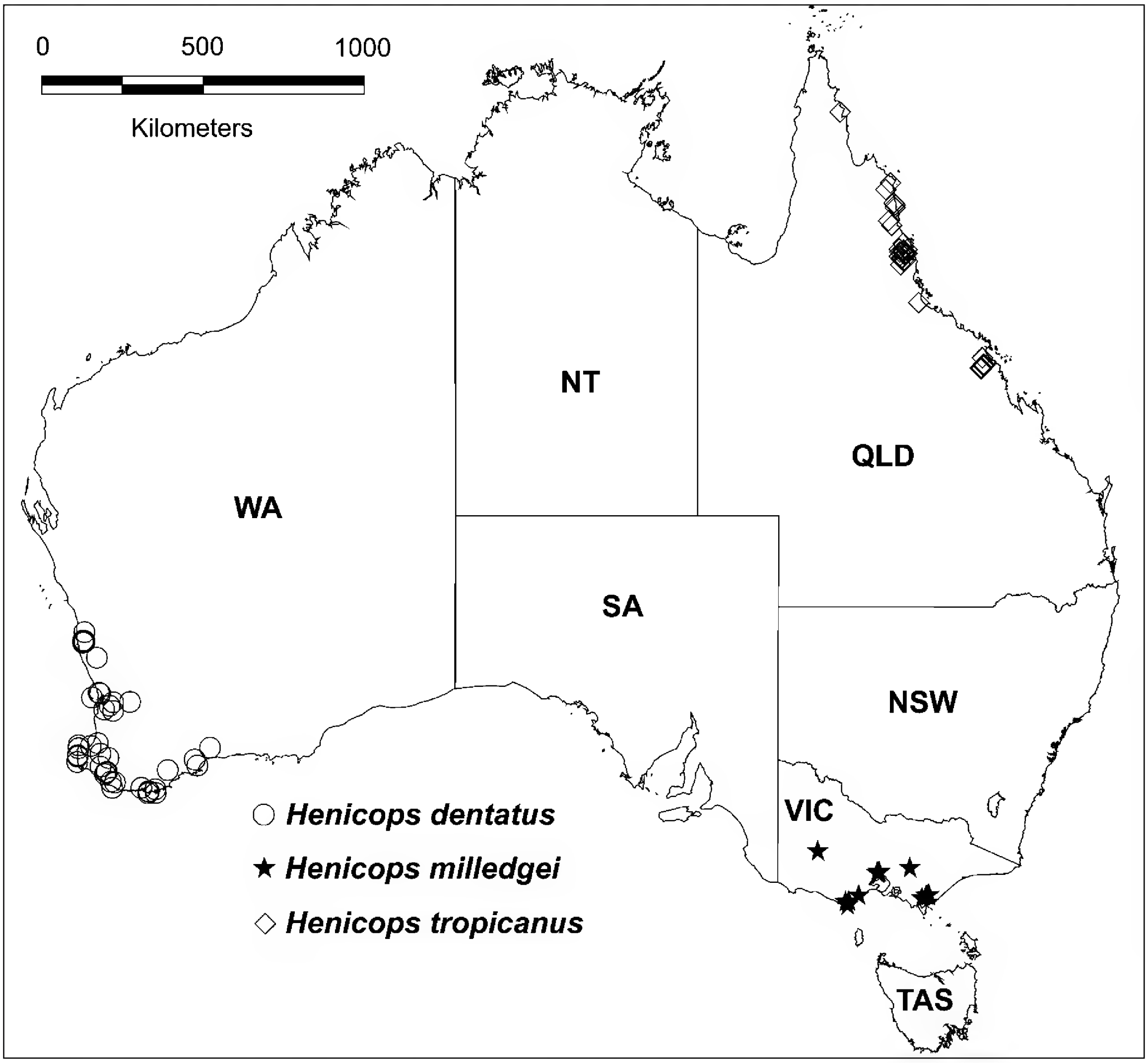

Fig. 1. Distribution of *Henicops dentatus* Pocock, 1901, *H. milledgei* n.sp. and *H. tropicanus* n.sp.

Systematics

Chilopoda Latreille, 1817
Order Lithobiomorpha Pocock, 1902
Family Henicopidae Pocock, 1901b
Subfamily Henicopinae Pocock, 1901b
Tribe Henicopini Chamberlin, 1912

Henicops Newport, 1844

Type species. *Henicops maculatus* Newport, 1844; by original designation.

Diagnosis. Member of *Lamyctes-Henicops* Group with 29–51 antennal articles; maxillipede coxosternum subtrapezoidal, dental margin moderately wide, with 3+3 or 4+4 teeth (exceptionally up to 6+6), lacking pseudoporodont; mandibular aciculae abundant, arranged in two (inner and outer) rows; several laciniate or plumose setae amidst simple setae on coxal process of first maxilla; projections on (at least) tergites 9, 11 and 13; last distal spinose projection of tibia on leg 14; subdivision of basitarsus of legs 1–12 indicated by paired larger setae; tarsi of legs 13 and 14 divided into three or four tarsomeres; distitarsus of leg 15 divided into at least two tarsomeres; first genital sternite of male divided longitudinally into two sclerites; male and female gonopods abundantly setose, with numerous distally curved setae on male gonopod.

Assigned species. *Lamyctes brevilabiatus* Ribaut, 1923; *Henicops dentatus* Pocock, 1901a (=*H. oligotarsus* Attems, 1911, n.syn.); *H. milledgei* n.sp.; *H. tropicanus* n.sp.

Discussion. The genus *Henicops* was erected by Newport (1844), with his concept of *Henicops* corresponding to the modern concept of the family Henicopidae. Two species of *Henicops* were originally named, *Henicops maculatus* from Tasmania and *H. emarginatus* Newport, 1844, from New Zealand. The latter was subsequently transferred to *Lamyctes* Meinert, 1868, and is a senior subjective synonym of the type species, *L. fulvicornis* Meinert, 1868 (Eason, 1996).

In erecting a new genus, *Paralamyctes*, Pocock (1901b) rediagnosed *Henicops* with emphasis on the division of the tarsi into tarsomeres. *Henicops* was again rediagnosed by Archey (1917), who included in that diagnosis the presence of plumose setae on the coxal process of the first maxilla, a character previously used to distinguish Lithobiidae from Henicopidae (Chamberlin, 1912). The "plumose" setae on the coxal process of the first maxilla in *Henicops* vary from laciniate (Fig. 15J; Edgecombe *et al.*, 2002: fig. 8H for *H. maculatus*) to plumose, though the latter differ in detail from the complex plumose setae of lithobiids (Edgecombe & Hollington, 2002: fig. 9C,E). The present study frames the generic diagnosis around synapomorphies that identify *Henicops* as a monophyletic group within a clade that also includes *Lamyctes* (=*Lamyctinus* Silvestri, 1909a; see Edgecombe & Giribet, 2003a), *Lamyctopristus* Attems, 1928, *Analamyctes* Chamberlin, 1955, *Easonobius* Edgecombe, 2003a, and apparently *Pleotarsobius* Attems, 1909. The monophyly of this *Lamyctes-Henicops* Group is strongly supported by sequence data from multiple molecular markers (Edgecombe *et al.*, 2002; Edgecombe & Giribet, 2003b), and notably by insertions in the 18S rRNA.

Henicops is united with the South African *Lamyctopristus* Attems, 1928 (Edgecombe, 2004a: fig. 34D) by the mandibular aciculae being divided into inner and outer rows (Figs. 5F, 10C). This two-row arrangement is associated with a larger number of aciculae (about 20) in *Henicops* than in allied henicopines. Previous diagnoses (Archey, 1917, 1937; Attems, 1928) cited three joints in legs 1–13 as diagnostic of *Henicops*, but this is now observed to pertain to most but not all species (at least two undescribed species have only two tarsomeres on legs 1–12). A more general characterization of the *Henicops* tarsal condition is that subdivision of the basitarsus of legs 1–12 is indicated by paired larger setae. Where the tarsus has only two tarsomeres, a pair of strong, divergent setae is situated on the basitarsus in the same position as those larger setae immediately proximal to the most proximal tarsomere articulation in species with three tarsomeres, i.e., the tripartite arrangement on the tarsi of legs 1–12 in *H. maculatus* and the three species described herein occurs by subdivision of the basitarsus. Concerning the distitarsus, all species of *Henicops* uniquely share a division of the distitarsus of leg 15 into tarsomeres, a state not otherwise developed in the Henicopini (see Table 1 for a comparison of tarsal segmentation between species). The bipartite first genital sternite in males (Figs. 6I, 11B, 16F) is invariant in *Henicops*. Elsewhere in Henicopidae, the division of this sternite into two sclerites is observed only in some members of *Lamyctes*, in those mostly African species split off by Verhoeff (1941) as *Metalamyctes*. The abundance of setae on the gonopods in both sexes is added to the generic diagnosis here, the number of setae in *Henicops* substantially exceeding that in most other Henicopinae, including other members of the *Lamyctes-Henicops* Group. This abundance could be explicitly defined in terms of the male gonopod having about 15 setae on the basal article and about 10 on the second and third. Among these are many distally curved setae (Figs. 4E, 12C).

Table 1. Tarsal segmentation in *Henicops*, showing number of tarsomeres in basitarsus and distitarsus (e.g., 2/1 indicates two segments in basitarsus and one in distitarsus).

	1–12	13	14	15
Henicops maculatus	2/1	2/2	2/3	2/4(5)
Henicops dentatus	2/1	2/2	2/2	2/3
Henicops tropicanus	2/1	2/2	2/2	2/3
Henicops milledgei	2/1	1/2	1/3	1/4

Additional distinction from *Lamyctes* is provided by the presence of tergal projections, subdivision of the tarsi, and a wider dental margin of the maxillipede coxosternum. A species that presents incongruence is the New Caledonian *Lamyctes brevilabiatus* Ribaut, 1923. Sequences from nuclear ribosomal as well as mitochondrial markers, separately as well as in combination, indicate that this species is more closely related to *Henicops* than to *Lamyctes* (Edgecombe & Giribet, 2003a,b). The molecular data more precisely indicate an alliance with members of the *Henicops dentatus* Group as defined below. Apomorphic morphological characters shared with *Henicops* include the relatively large number of antennal articles (38–47), a relatively wide dental margin of the maxillipede coxosternum with 3+3 teeth and no pseudoporodont, laciniate setae on the coxal process of the first maxilla, and a bipartite first genital sternite in the male (AM KS82626, Mt Humboldt). The spines beneath the posterior pretarsal accessory claw are short, as in *Henicops* (Fig. 14L), rather than long and needle-like as in *Lamyctes* (Edgecombe & Giribet, 2003a: figs. 34, 36). The New Caledonian species lacks, however, several characters shared by all other members of *Henicops*. It has transverse (rather than projected) posterior margins of TT11 and 13, the last distal spinose projection is on the tibia of leg 13 (rather than 14), and the tarsi of legs 13–15 are bipartite, with no trace of a subdivision of either tarsomere. Legs 1–12 have indistinct tarsal articulations. The mandible differs from other members of *Henicops* in having relatively few (nine) aciculae in a single row (Fig. 2B,C), rather than having about 20 aciculae in two rows. Cladistic analysis of morphological evidence resolves *brevilabiatus* as sister group of *Henicops* as diagnosed above in some minimal length cladograms, but as a member of *Lamyctes* in others, whereas combination of the morphological data with molecular data favours an ingroup position within *Henicops* (Edgecombe & Giribet, 2003b). Based on strength of the molecular support together with the presence of several apomorphies of *Henicops* listed above, the species is reassigned to *Henicops*.

Henicops dentatus Group

Diagnosis. *Henicops* with 29–40 (most commonly 36) antennal articles, with a relatively gradual change in length of articles along antenna; Tömösváry organ deep, outer edge at margin of cephalic pleurite; TT7, 9, 11 and 13 with subquadrate emargination (posterior margin with transverse medial sector with independent curvature from lateral sectors); three moderate sized teeth on dental margin of maxillipede coxosternum; groove in accessory denticle field lacking on mandibular teeth; mandibular aciculae variable in structure, differentiated into some with pronounced serrations on both margins and others with a simple margin along most or all of length; ventral branching bristles of mandible lacking spine-like branches on basal part; three tarsomeres in legs 1–12; four tarsomeres in legs 13 and 14, basitarsus and distitarsus with two tarsomeres each; five tarsomeres in leg 15, basitarsus having two, distitarsus three.

Assigned species. *Henicops dentatus* Pocock, 1901a (=*H. oligotarsus* Attems, 1911); *H. tropicanus* n.sp.

Discussion. The diagnosis above lists characters that unite *Henicops dentatus* and *H. tropicanus* n.sp. that are either unique within *Henicops* or permit distinction from *H. maculatus* or other species. Several of these can be regarded as synapomorphies for *H. dentatus* and *H. tropicanus*.

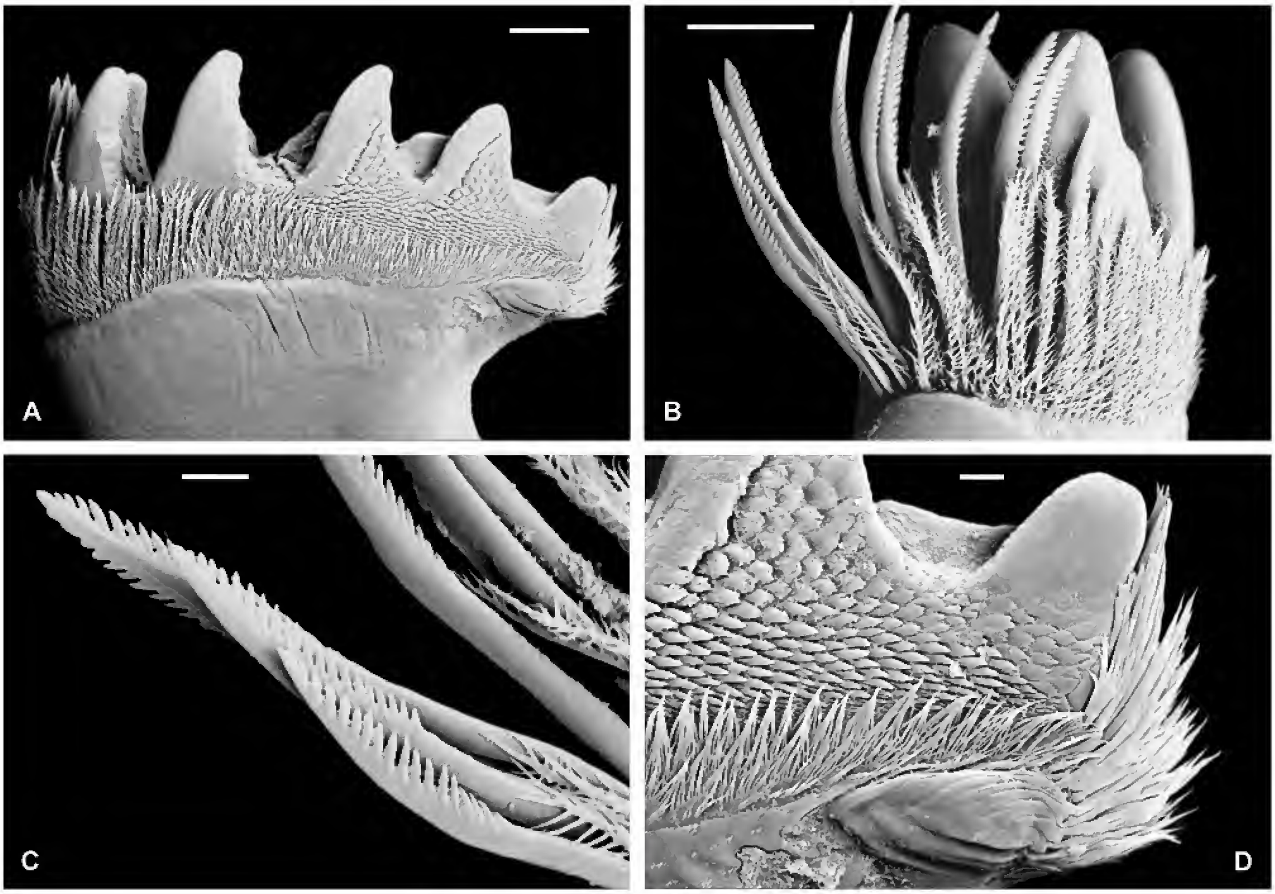

Fig. 2. *Henicops brevilabiatus* (Ribaut, 1923). QM S60651, ♀, Me Maoya, New Caledonia, mandible: (*A*) gnathal edge, scale 50 µm; (*B*) ventral part of gnathal edge, scale 50 µm; (*C*) aciculae, scale 10 µm; (*D*) dorsal teeth and furry pad, scale 10 µm.

Character polarity is evaluated in the context of *Henicops* being sister to a clade that includes *Lamyctes, Analamyctes, Easonobius* and *Lamyctopristus* (Edgecombe *et al.*, 2002; Edgecombe, 2003a, 2004a; Edgecombe & Giribet, 2003b) (see synoptic classification below).

Indistinct grooves in the accessory denticle field on the mandibles (Figs. 5D,I, 10A,F) are restricted to the *H. dentatus* Group within *Henicops*. Grooves or grooved ridges (see Fig. 14D,F for their presence in *H. milledgei*) are observed in most Henicopini, including other members of the *Lamyctes-Henicops* Group (Fig. 2A). The "notched" margin of tergite 7 in the *H. dentatus* Group (Figs. 3, 7A) is distinctive for those two species within *Henicops*, though the same shape of this tergite is observed in some other Henicopinae, e.g., within *Paralamyctes* and in Zygethobiini. Tergite shapes were noted by Pocock (1901a) as subquadrately emarginate TT7, 9, 11 and 13, serving as a distinguishing character of *H. dentatus* and *H. tropicanus* relative to *H. maculatus* and *H. milledgei.*

A differentiation of the mandibular aciculae into an outer row with serrated margins and an inner row with simple or weakly scalloped margins (Figs. 5G, 10C,D) is shared with *Henicops milledgei* (Fig. 14I). This differentiation is apparently apomorphic relative to the uniform structure of the aciculae in *H. maculatus* (Edgecombe *et al.*, 2002: fig. 5C) and *H. brevilabiatus* (Fig. 2B), the latter being shared by outgroups. Likewise, *H. milledgei* and the *H. dentatus* Group share a narrow base to the ventralmost bristles in the fringe of branching bristles along the mandibular gnathal edge. These bristles have no or few spine-like projections

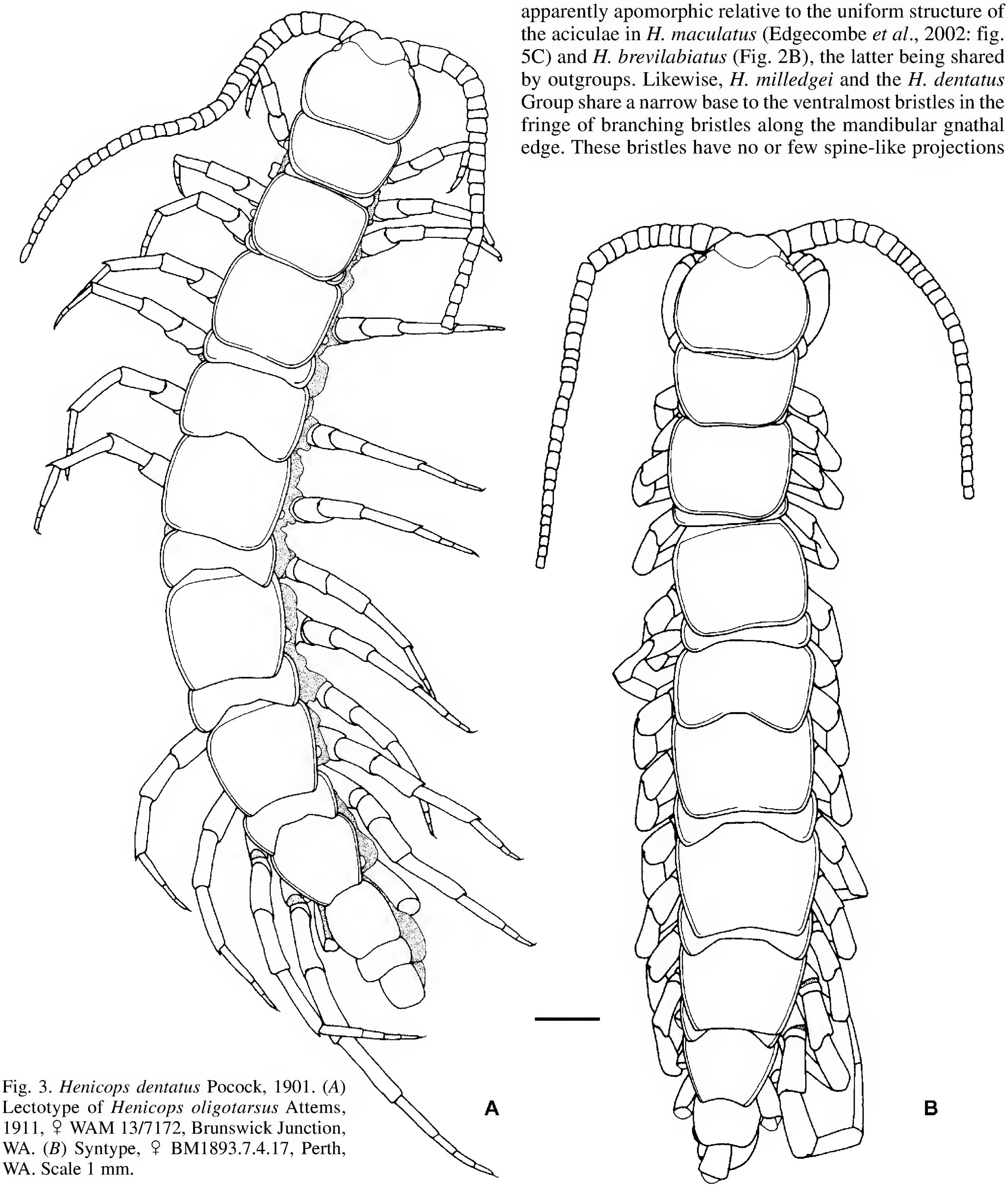

Fig. 3. *Henicops dentatus* Pocock, 1901. (*A*) Lectotype of *Henicops oligotarsus* Attems, 1911, ♀ WAM 13/7172, Brunswick Junction, WA. (*B*) Syntype, ♀ BM1893.7.4.17, Perth, WA. Scale 1 mm.

basally (the entire basal half of the bristle lacks spines in *H. dentatus*: Fig. 5H), but branch evenly along their distal part (Figs. 10E, 14H). This is also apparently apomorphic relative to the evenly spine-covered bristles in H. maculatus (Edgecombe *et al.*, 2002: fig. 5C), which have spines on their bases. The latter state is possessed by other taxa in the *Lamyctes-Henicops* Group (for *Lamyctes*, see Edgecombe *et al.*, 2002: fig. 6D, Edgecombe & Giribet, 2003a: fig. 27; Fig. 2B herein for *H. brevilabiatus*) and other Henicopini generally.

The relatively even length of the antennal articles in the *H. dentatus* Group is potentially apomorphic relative to the groups of shortened articles occurring in pairs in other congeners because other genera of the *Lamyctes-Henicops* Group (e.g., *Lamyctes, Analamyctes, Easonobius, Lamyctopristus*) have the paired, shortened articles. The deep, submarginally positioned Tömösváry organ in the *H. dentatus* Group (Figs. 6L, 9D–F) is unique within *Henicops*, but is shared by most non-*Henicops* Henicopini. The deep, submarginal organ is thus apparently plesiomorphic relative to the shallow organ situated medially on the cephalic pleurite in *H. maculatus* (Edgecombe *et al.*, 2002: fig. 1G) and *H. milledgei* (Fig. 15D,E). This character suggests that the *H. dentatus* Group is possibly sister to all other species of *Henicops*.

Henicops dentatus **Pocock, 1901**

Figs. 3–6

Henicops dentatus Pocock, 1901a: 454.
Henicops oligotarsus Attems, 1911: 150; **new synonym**.
Henicops oligotarsus.–Borucki, 1996: fig. 102.

Diagnosis. Member of *Henicops dentatus* Group with female gonopod having two small, bullet-shaped or distally truncated spurs; outer spur up to 50% wider than inner spur; branching bristles on mandibular gnathal edge narrow in dorsal part of fringe; ventral bristles in fringe lacking spines on their basal third or more.

Type material. SYNTYPES: BM1893.7.4.17, ♀ (Fig. 3B), BM1893.7.4.18, ♂, Perth, WA, H.W.J. Turner.

Other material. Types of *Henicops oligotarsus* Attems, 1911: LECTOTYPE: WAM 13/7172 (Fig. 3A), ♀, Brunswick Junction, WA (station 139 of Michaelsen & Hartmeyer, 1907), 33°15'S 115°50'E, W. Michaelsen & R. Hartmeyer, 7 Oct 1905, designated here. A lectotype is selected to fix the name to a single type locality; the chosen specimen is the most intact large individual from a locality represented by both sexes in the WAM and NMV. PARALECTOTYPES: WAM, 2♂♂, from type locality. NMV: 3907, 1♀, Boyanup (station 146); 3908, 1♀, 2♂♂, Brunswick (station 139); 3909, 1♀, Albany (station 165). ZIUM: 6♀♀, 2♂♂, Lion Mill (station 99); 1♀, 1♂, Mundaring Weir (station 101); 1♂, Bridgetown (station 144); 1♀, Beverly (station 156). Attems (1911) listed additional syntypes from Wooroloo, East Fremantle, Jarrahdale, and Gooseberry Hill that we have not located.

WESTERN AUSTRALIA: WAM: 25/822, 1♀, Dandaragan, 30°40'S 115°42'E, L. Glauert, Sep 1925; 28/740, 1♂, Serpentine, 32°22'S 115°58'E, L. Glauert, Aug 1928; 14/987, 1♀, Denmark, 34°57'S 117°21'E, W.B. Alexander, May 1914; T42434, 4♀♀, 1♂, Hepburn Heights, 31°49'02"S 115°46'13"E, MSH & JMW, 13 Jul–25 Sep 1995; T42435, 3♀♀, Warwick Open Space, 31°50'34"S 115°48'50"E, MSH & JMW, 25 Sep–28 Nov 1995; T42436, 7♀♀ (Figs. 4F, 5F–I, 6H), 2♂♂ (Fig. 4E), Warwick Open Space, 31°50'33"S 115°49'00"E, MSH & JMW, 25 Sep–28 Nov 1995; T42437, 1♀, Balannup Lake, Gosnells, E.G. Cockett, 24 Dec 1968; T42438, 1♀, Bald Head, Albany, D.D. Giuliani, 10 May 1969; T42439, 1♂, Bentley, B. Anderson, 8 Sep 1976; T42440, 1♀, Boranup, G.M. Riley, 10 Sep 1965; T42441, 1♂, Peppermint Forest, 5 mi N Busselton, R.J. McKay & R.W. George, 22 Oct 1969; T42442, 1♀, T42443, 1♀, Cape Freycinet, 34°06'S 114°59'E, T.F. Houston, 15–18 Nov 1986; T42444, 1♂, Cape Naturaliste NP, catchment of Yallingup Brook, 33°38'50"S 115°02'10"E, J. Mitchell *et al.*, 1–10 Dec 2000; T42445, 1♀, Fossil Deposit SF, 4 mi W cape, G.H. Riley & G. Kendrick, 8 Sep 1969; T42446, 1♀, Cocanarup Timber Reserve, 33°38'S 119°54'E, G. Harold, Nov 1993; T42447, 1♂, Worsley Alumina Project, Collie off Fletcher Rd, D. Walford & M. Sawle, Jul 1980; T42448, 1♀, Crowea, S.J. Curry, 31 Oct 1980; T42449, 1♂, Dog Pool on Shannon River, 34°46'S 116°22'E, MSH & JMW, 27–30 Apr 1990; T42450, 1♀, 3 km N Dog Pool, 34°45'S 116°13'E, MSH & JMW, 30 Apr 1990; T42451, 4♀♀, 3♂♂, Dwellingup, J.D. Majer, 7–25 Nov 1975; T42452, 1♀, R.G.C. Mineral Sands, 10 km S Eneabba, 29°50'S 115°15'E, L.P. McMillan & P. West, 22 Jul 1997; T42456, 5♀♀, 1♂, Fitzgerald River NP, West Mt Barren, NE slope, 34°13'S 119°26'E, MSH & JMW, 28 May 1994; T42457, 1♀, Fitzgerald River NP, Twertup, 34°01'S 119°20'E, MSH & JMW, 29 May 1994; T42458, 1♂, "Glenbourne", Old Ellens Brook Rd, 33°53'S 115°00'E, L. Marsh *et al.*, 27–28 Oct 1996; T42459, 1♂, "Glenbourne", Spring Rd S Gracetown, 33°53'S 115°00'E, 28–30 Jun 1997, L.M. Marsh *et al.*; T42460, 1♂, "Glenbourne", S Gracetown, 33°54'32"S 115°00'24"E, L. Marsh *et al.*, 30 Oct–1 Nov 1999; T42461, 1♂, Gleneagle, 32°15'S 116°10'E, J.A. Springett, 22 Oct 1971; T42463, 1♀, 12.5 mi NE Katanning, E.J. Car and G.M. Riley, 28 Oct 1964; T42464, 1♂, Leeman, R.P. McMillan, 31 Aug 1981; T42465, 1♀, T42466, 1♀, Ludlow Tuart Forest, 33°34'S 115°29'E, J.A. Springett, 31 Aug 1971; T42467, 4♀♀, Margaret River, L.E. Koch, 22–24 Aug 1973; T42468, 1♀, T42469, 1♂, 6.5 km and 5.5 km NW Meelup, 33°33'00"S 115°01'45"E, G.A. Harold, 22–27 Oct 1985; T42470, 1♂, Mt Cooke, near summit, 32°25'S 116°18'E, MSH, JMW & M. Peterson, 7 Aug 1990; T42471, 1♂, same locality, MSH & JMW, 1 Oct 1990; T42472, 1♀, same locality and collectors, 16 Dec 1990; T42473, 2♀♀, same locality, 31 Jul 1991; T42474, 1♀, same locality, 19 Sep 1991; T42475, 1♀, 1♂, base of Mt Dale, W side, 32°08'S 116°18'E, JMW *et al.*, 27 Sep 1998; T42477, 1♂, T42478, 1♀, T42479, 1♂, T42485, 1♂, c. 4 km NNE Mt Lesueur, 30°08'S 115°12'E, K. Gaull *et al.*, 9–12 Jul 1989; T42481, 1♂, 1.6 km N Mt Lesueur, 30°10'S 115°12'E, K. Gaull *et al.*, 11 Jul 1989; T42482, 1♀, c. 5 km NE Mt Lesueur, 30°09'S 115°15'E, K. Gaull *et al.*, 9 Jul 1989; T42486, 2♂♂, 7 km NE Mt Lesueur, 30°07'S 115°15'E, K. Gaull *et al.*, 1989; T42487, 1♀, 4.5 km E Mt Peron, 30°06'S 115°12'E, K. Gaull *et al.*, 7 Jul 1989; T42488, 1♂, North Tarin Rock Reserve, D. Kitchener *et al.*, 17–27 May 1971; T42489, 1♀, Pemberton, Allis Rd, 34°30'S 116°00'E, J.A. Springett, 9 Nov 1971; T42490, 1♂, Bluff Knoll, Stirling Ranges, D.D. Giuliani, 13 May 1969; T42491, 2♂♂, Stirling Range NP, Ellen Peak, 34°21'32"S 118°19'45"E, 1000 m, S. Barrett, 4 Apr 1995; T42492, 4♂♂, Swan River Dist, 15–18 Jul 1924; T42493, 1♀, The Cascades, 8 km SSW Pemberton, 34°30'S, 116°00'E, MSH & JMW, 3 May 1990; T42494, 1♂, Torbay hill, boundary track, 35°05'S 117°37'E, B.Y. Main, 20 Feb–6 Mar 1983; T42495, 1♂, Torbay Head, 35°05'S 117°38'E, B.Y. Main, 9 Aug–7 Sept 1985; T42496, 1♀, Torbay Head, B.Y. Main, 20 Jun 1986; T42497, 1♂, Torndirrup NP, Sharp Point Rd, 35°06'42"S 117°52'55"E, JMW, 14 Nov 1998; T42498, 1♀, Two People Bay, G. Smith, 15 Sep 1976; T42499, 1♀, Tutanning Reserve, Pingelly, E. Mercer, 28 Aug 1980; T42500, 1♂, Walyunga NP, M. Archer & E. Jeffreys, 4 May 1969; T42501, 1♀, Wanneroo, 33°54'32"S 115°00'24"E, R.P. McMillan, 18 Aug 1952; T42502, 1♀, West Cape Howe NP, Lake William, 35°04'S 117°37'E, B.Y. Main, 26 Mar–5 Apr 1985; T42503, 1♀, West Cape Howe NP, West Cape Howe, 35°08'S 117°36'E, B.Y. Main, 15–24 Jan 1988; WAM, 1♀, 1♂, Rottnest Island, Mt Herschell, 31°59'S 115°31'E, L. Glauert, Sep 1927.

AUSTRALIAN MUSEUM: KS15269, 3♀♀, 2♂♂, Dombalup SF, Marri Rd, 34°30'S 116°00'E, M.R. Gray, 15 Jan 1979; KS15361 (Fig. 4A–D), c. 200 individuals, Treen Brook SF, 8 km W Pemberton, 34°26'S 116°04'E, M.R. Gray, 13 Feb. 1979; KS35584, 1♀, 3♂♂, Walpole-Nornalup NP, 34°57'S 116°16'E, M.R. Gray, 15 Feb 1979; KS35644, 1♀, 2♂♂, Pine Ck, 0.5 km from Quarty Rd, Nannup-Pemberton area, 34°15'S 115°50'E, M.R. Gray, 14 Feb 1979; KS77589, 1♂, Pemberton Forest Park, Karri Bush Walk, 34°27'S 116°01'30"S E, G.D. Edgecombe & Z. Johanson, 23 Feb 2001; KS83629, 1♀ (Fig. 6G,M), KS83630, 1♂ (Figs. 5A–E,J–O, 6A–F,I–L), Gloucester NP, crossing of Bibbulmun Track and Burma Rd, 34°27'S 116°03'E, G.D. Edgecombe & Z. Johanson, 23 Feb 2001.

CALIFORNIA ACADEMY OF SCIENCES (leg. E.S. Ross & D. Cavagnaro): 2♀♀, 3♂♂, Darlington, 450 ft, 5 Sep 1962; 1♀, 20 mi S Borden, 200 m, 23 Sep 1962; 1♀, 25 mi NW Walpole, 100 m, 25 Sep 1962; 4♀♀, 2♂♂, Cape Naturaliste, 5 m, 27 Sep 1962; 1♂, 7 mi NE Busselton, 50 m, 28 Sep 1962.

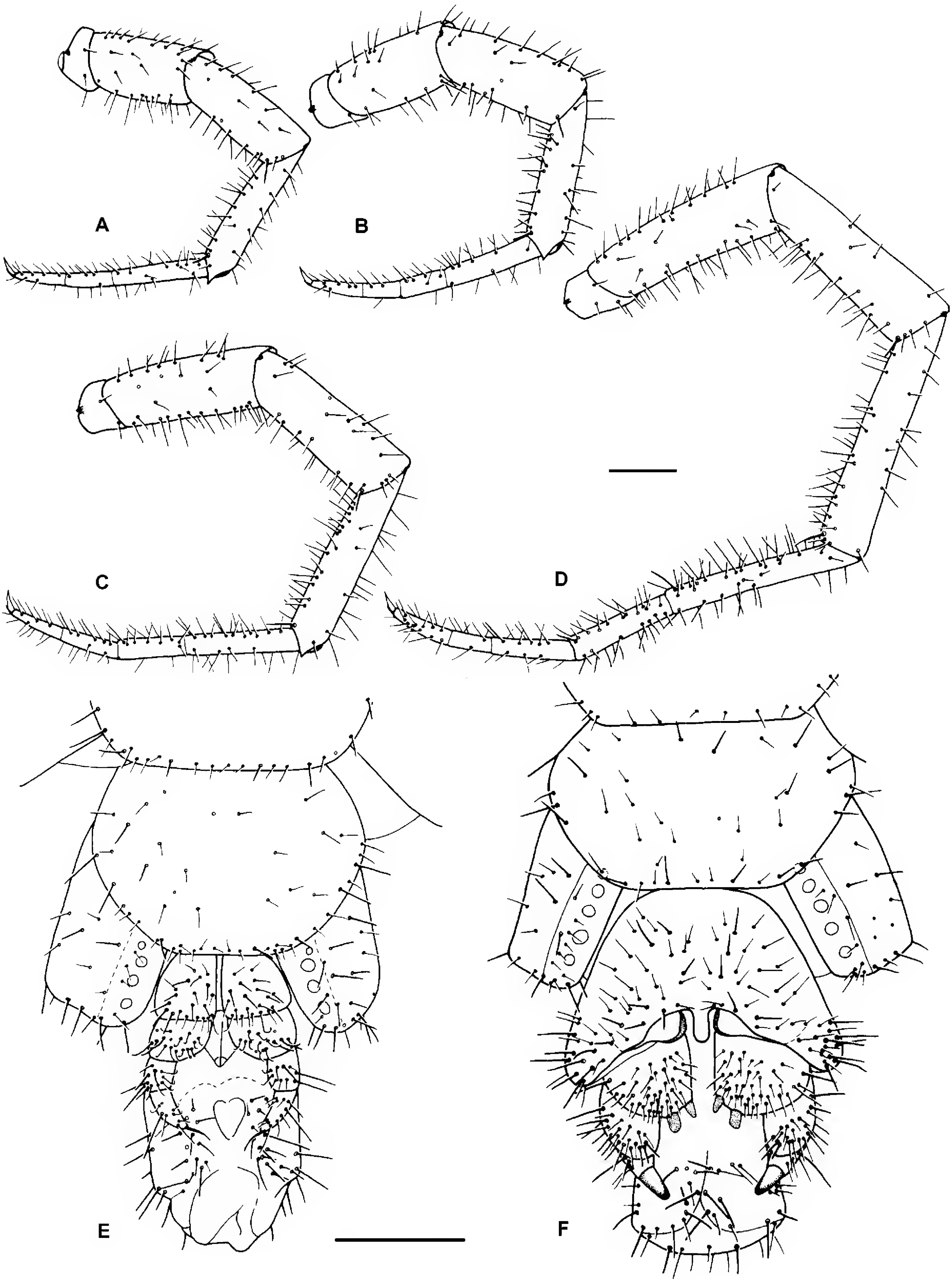

Fig. 4. *Henicops dentatus* Pocock, 1901. (*A–D*) ♀ AM KS15361, Treen Brook SF, W Pemberton, WA: (*A*) leg 12; (*B*) leg 13; (*C*) leg 14; (*D*) leg 15. (*E,F*) ♂, ♀, WAM T42436, terminal segments and gonopods, Warwick Open Space, WA. Scales 0.5 mm.

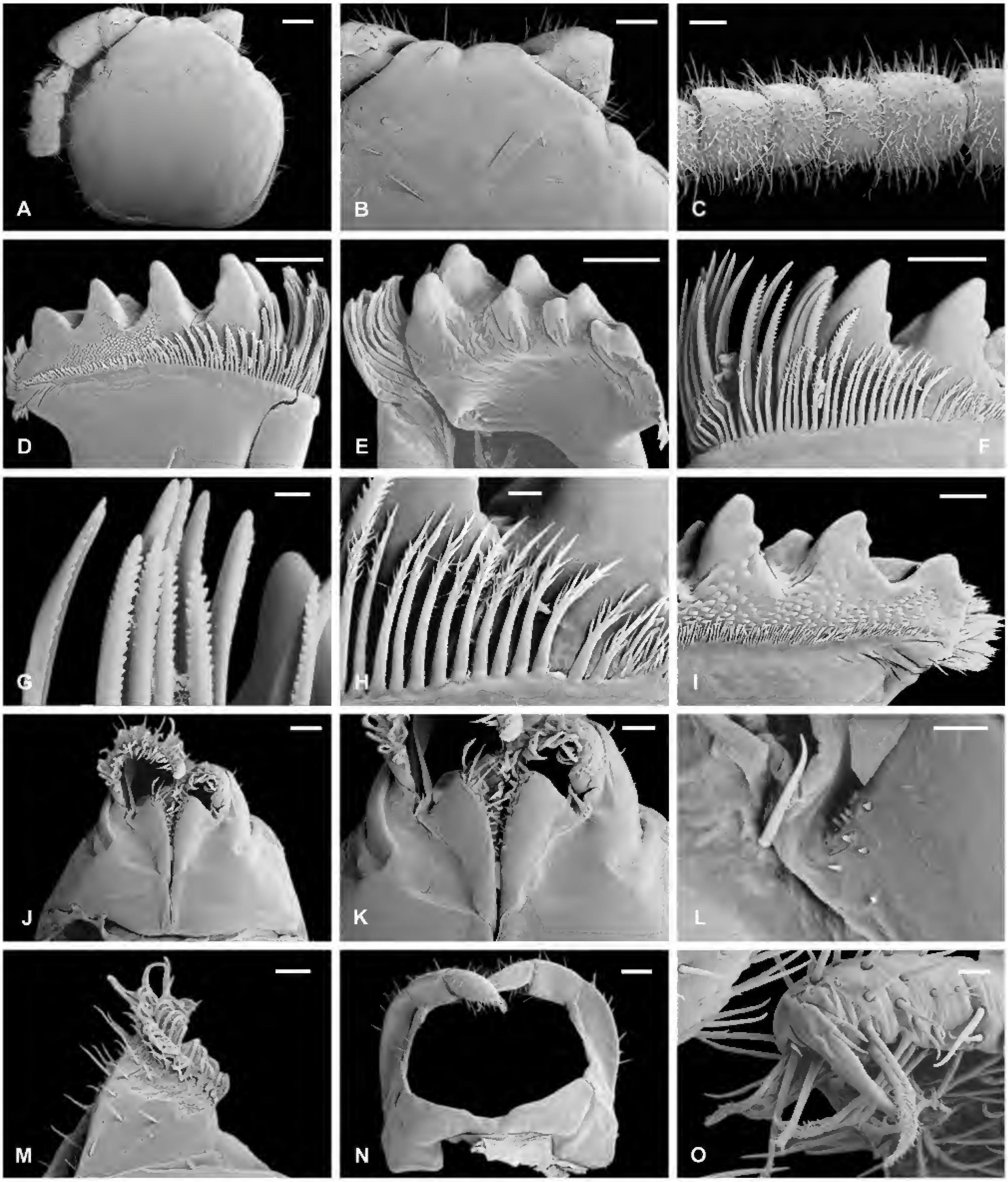

Fig. 5. *Henicops dentatus* Pocock, 1901. (*A–E, J–O*) ♂ AM KS83630, Gloucester NP, Pemberton, WA: (*A*) dorsal view of head shield, scale 60 µm; (*B*) anterior part of head shield, showing transverse and antennocellar sutures, scale 50 µm; (*C*) antennal articles, scale 100 µm; (*D,E*) outer (anterior) and inner (posterior) views of gnathal edge of right mandible, scales 60 µm, 50 µm; (*J*) first maxillae, scale 130 µm; (*K*) coxal processes of first maxillae, scale 60 µm; (*L*) cluster of sensilla microtrichoidea between telopodite and coxal process of first maxilla, scale 15 µm; (*M*) distal article of telopodite of first maxilla, scale 60 µm; (*N*) second maxillae, scale 300 µm; (*O*) tarsus and pretarsus (claw) of second maxilla, scale 20 µm. (*F–I*) ♀ WAM T42436, Warwick Open Space, WA, left mandible: (*F*) ventral part of gnathal edge, scale 50 µm; (*G*) aciculae, scale 10 µm; (*H*) fringe of branching bristles, scale 10 µm; (*I*) dorsal teeth and furry pad, scale 30 µm.

Distribution. Southwest Western Australia, north to Eneabba (29°50'S 115°15'E), east to Cocanarup (33°38'S 119°54'E) (Fig. 1), sclerophyll forest.

Discussion. *Henicops dentatus* is identical to or within the range of variation of *H. tropicanus*, described in full below, in most respects except for the female gonopods and details

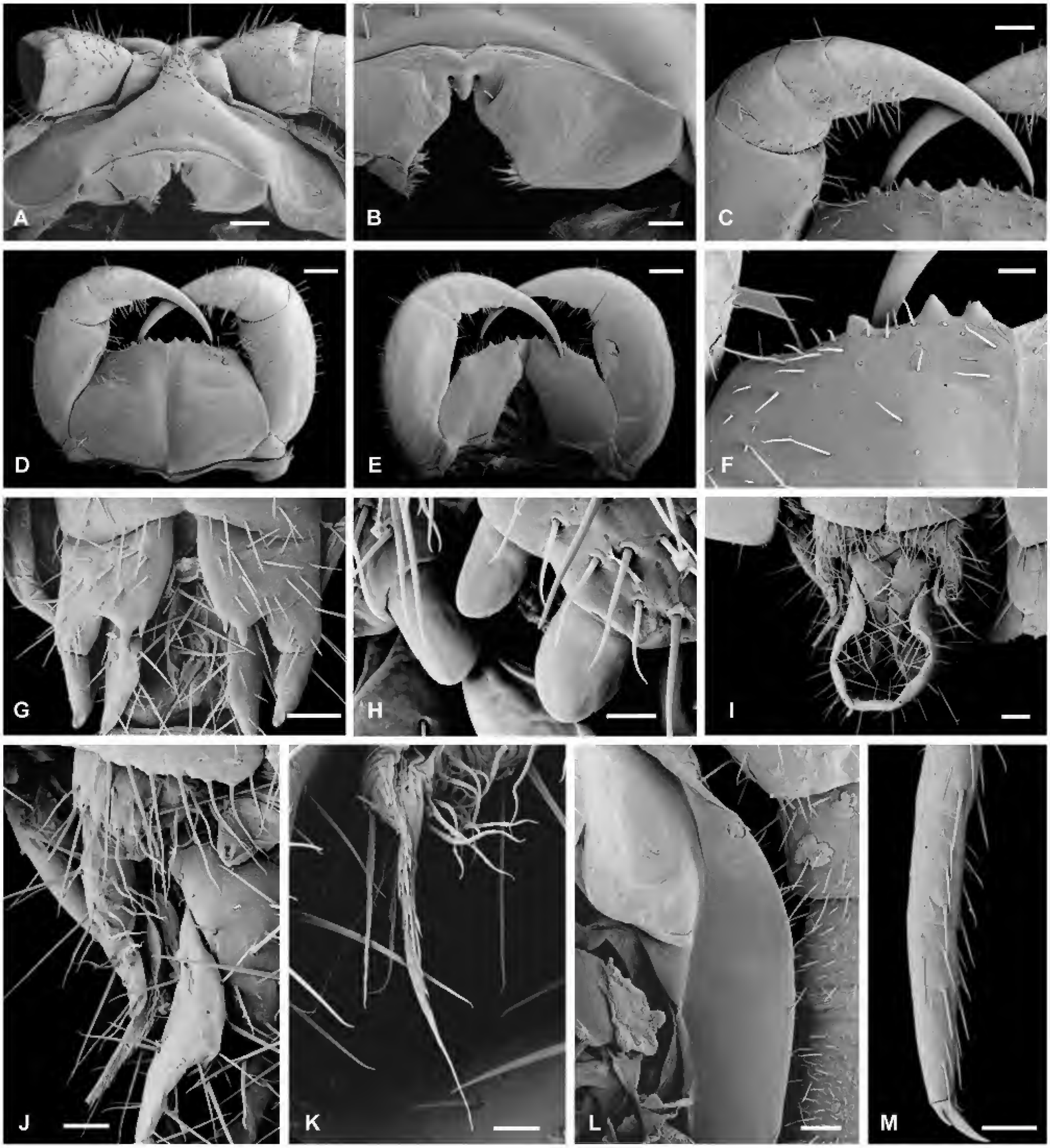

Fig. 6. *Henicops dentatus* Pocock, 1901. (*A–G,I–M*) Gloucester NP, Pemberton, WA. (*A–F,I–L*) ♂ AM KS83630: (*A*) clypeus and labrum, scale 180 µm; (*B*) labrum, scale 70 µm; (*C*) telopodite and dental margin of maxillipede, scale 180 µm; (*D,E*) ventral and dorsal views of maxillipede, scales 300 µm; (*F*) dental margin of maxillipede coxosternum, scale 70 µm; (*I,J*) gonopods and detail of right gonopod and penis, scales 100 µm, 30 µm; (*K*) terminal process of gonopod, scale 30 µm; (*L*) cephalic pleurite, showing Tömösváry organ, scale 100 µm. (*G,M*) ♀ AM KS83629: (*G*) gonopods, scale 100 µm; (*M*) tarsus and pretarsus of leg 12, scale 70 µm. (*H*) ♀ WAM T42435, Warwick Open Space, WA. Spurs on gonopods, scale 30 µm.

of the mandibular gnathal edge. Distinction between the two is discussed under the latter species.

The present study of a large sample of southwest Western Australian specimens of *Henicops*, including the syntypes of both *H. dentatus* and *H. oligotarsus*, corroborates Archey's (1937) suspicion that the two named Western Australian species are synonymous. When naming *H. oligotarsus*, Attems made no mention of the previously named *H. dentatus*. Attems (1928:63) later acknowledged *H. dentatus* in a key to *Henicops* species. He distinguished the two Western Australian species on the basis of tergites 7, 9, 11 and 13 of *H. oligotarsus* being "toothed" and the corresponding tergites of *H. dentatus* and *H. maculatus* being "rounded", in addition to leg 15 of *H. oligotarsus* having five tarsomeres as opposed to six tarsomeres in *H. dentatus* and *H. maculatus*. Both of these alleged differences are unfounded. Description of a "toothed" condition of tergites in *H. oligotarsus* refers to the triangular projections of the posterior angles of TT7, 9, 11 and 13. This is a more or less accurate description of the tergites of Attems' specimens (Fig. 3A), but it is identical to the condition of these tergites in the types of *H. dentatus* (Fig. 3B). Indeed, no *Henicops* specimens from anywhere in the range of *H. dentatus* (=*H. oligotarsus*) have tergites 7, 9, 11 and 13 that could be described as "rounded". Leg 15 of all Western Australian specimens has five tarsomeres (Fig. 4D) so no specific distinction can be made based on some specimens having five and others having six. The types of *H. dentatus* lack legs 14 and 15 (and seemingly lacked these legs when Pocock described the species, for no mention was made of them), so Attems' claim of a difference from *H. oligotarsus* has no basis. In the absence of any morphological characters to support the presence of multiple taxa in Western Australia, all specimens are recognized as a single species, using the older name, *H. dentatus*. The description of *H. oligotarsus* (Attems, 1911:150) stated that the species has 33–35 antennal articles but among the syntypes are large specimens with 29–36 articles. Other collections extend the range to 38 articles, though as in *H. tropicanus* the most common number is 36.

Henicops tropicanus n.sp.

Figs. 7–11

Etymology. For the Wet Tropics of northeastern Queensland, where the species occurs.

Diagnosis. Member of *Henicops dentatus* Group with female gonopod having two (exceptionally three) large, elongate, bullet-shaped spurs; legs 14 and 15 relatively sparsely setose, with few setae on tibia and basitarsus of leg 15.

Type material. HOLOTYPE: ♀ QM S39941 (Fig. 7A), from head of Roots Creek, 12km WNW Mossman, Queensland, 16°24'46"S 145°16'03"E, 1200 m, 28 Dec 1989–11 Jan 1990, ANZSES, pitfall. PARATYPES: ♂ QM S39941, from type locality, collection data as for holotype; S39869, 3♀♀, S39873, 1♂, S39898, 2♀♀ (Figs. 8A–D, 10D–F,K, 11C,H,J), 1♂ (Figs. 9B–D,F–J, 10A–C,G–H,J,M, 11D,E,I), S39934, 2♀♀, Mossman Bluff Track, 5–10 km W Mossman, GBM, G. Thompson & ANZSES, 20 Dec 1989–15 Jan 1990.

Other material. QUEENSLAND: QM: S22632, 1♀, 14.4 km N Wudjl Wudjl, 15°52'S 145°19'E, R. & S. Raven, P. & E. Lawless, 28 Nov 1992–18 Apr 1993; S39861, 2♀♀, 1♂, Mt Dalrymple, 21°03'S 148°38'E, 1200 m, ANZSES, 21 Dec 1992–10 Jan 1993; S39863, 1♂, Eungella, Pease's Lkt, 21°07'S 148°31'E, 900 m, D. Cook & GBM, 17 Nov 1992–Apr 1993; S39866, 2♀♀, S39899, Maalan Rd, 2 km S Palmerston Hwy, 17°36'S 145°42'E, 750 m, GBM & J. Hasenpusch, 10 Jan–7 Mar 1995; S39870, 1♀, Wongabel SF, 17°19'30"S 145°29'45"E, R. Raven, P. & E. Lawless & M. Shaw, 23 Jul–26 Nov 1992; S39872, 2♀♀, Longlands Gap SF, 17°27'30"S 145°28'45"E, R. Raven, P. & E. Lawless & M. Shaw, 23 Jul–26 Nov 1992; S39874, 1♀, 1♂, S39875, Karnak-Devils Thumb, 8–12 km NW Mossman, 1100 m, ANZSES, 26 Dec 1989–15 Jan 1990; S39884, 2♀♀, 4♂♂, Hughes Rd, Topaz, 17°26'S 145°42'E, 650 m, GBM & Breeden, Sep–Dec 1993; S39930, 1♂, same locality, GBM, D. Cook & H. Jantezki, 6 Dec 1993–25 Feb 1994; S39892, 4♀♀, Kjelberg Rd turnoff, 17°32'S 145°36'E, 850 m, GBM & J. Hasenpusch, 7 Mar–15 May 1995; S39961, 2♀♀, same locality, 25 Nov 1994, 10 Jan 1995; S39896, 4♀♀, Kjelberg Rd, Mt Fisher, 17°32'S 145°33'E, 1000 m, J. Hasenpusch, 1 Dec 1993–25 Feb 1994; S39902, 1♀, S39962, 1♀, Big Tableland, 15°43'S 145°17'E, 740 m, ANZSES, 20 Dec 1990–8 Jan 1991; S39906, 1♀, Eungella NP, Mt William, 21°02'S 148°36'E, 1200 m, GBM, 19 Apr 1979, rf; S39924, 1♀, 1♂, Pandanus Ck, Cathu SF, 20°48'S 148°33'E, 80 m, GBM, 22 Apr 1979; S39925, 4♂♂ (Fig. 7C), 2.5 km S Mt Hartley, 15°47'S 145°19'E, L. Roberts, 8 Dec 1993–2 Feb 1994; S39927, 2♀♀, 3 juveniles, Mt Fisher, 7 km SW Millaa Millaa, 17°33'S 145°33'E, 1000 m, GBM & D.K. Yeates, 3 May 1983, rf; S39928, 3♀♀, 3♂♂, Westcott Rd, Topaz, 17°25'S 145°42'E, 680 m, GBM, Jul–Dec 1993; S39940, 1♀, 2 km SE Mt Spurgeon via Mt Carbine, 16°27'S 145°12'E, 1100 m, GBM & G. Thompson, 20 Dec 1988, rf; S39946, 1♂, 2 juveniles, Mt Bartle-Frere, W base, 17°23'S 145°46'E, 700 m, GBM & J. Hasenpusch, 25 Nov 1994–10 Jan 1995; S39947, 2♀♀, 1♂, Lamins Hill, 17°22'S 145°42'E, 880 m, GBM & J. Hasenpusch, 1 Dec 1993–25 Feb 1994; S39954, 1♀, Eungella NP, Broken R, 21°10'S 148°30'30"E, P. Lawless, R. Raven & M. Shaw, 10 Nov 1991–29 Jul 1992; S39955, 1♀, same locality, 29 Jul–4 Dec 1992; S39956, 1♀, Malaan SF, 17°35'30"S 145°36'45"E, R. Raven, P. & E. Lawless & M. Shaw, 25 Jul–26 Nov 1992; S39967, 1♀, 1.5 km SE Mt William, 21°02'S 148°37'E, 1060 m, ANZSES, 21 Dec 1992–10 Jan 1993; S39973, 1♀, Malaan SF, V.E. Davies & R. Raven, 20–24 Apr 1978.

AUSTRALIAN MUSEUM: 1♂, Eungella NP, Broken River campsite, G.D. Edgecombe, 18 Apr 1998, rf; 1♀, KS83631, 2♂♂ (Figs. 9A,E,K–M, 10I,L, 11A,B,F,G,K), Eungella NP, Dalrymple Rd, 1.7 km and 2.9 km NE Snake Rd, G.D. Edgecombe, 21 Apr 1998, rf.

AUSTRALIAN NATIONAL INSECT COLLECTION: 2♀♀, 9 km ENE Mt Tozer (ex. Berl. 1059, 1062), 12°43'S 143°17'E, T. Weir, 10–16 Jul 1986; 2♀♀, juveniles, larval stadia LII–IV, 3 km NE Mt Webb (ex. Berl. 692, 721), 15°03'S 145°09'E, T. Weir, 1–3 Oct 1980, 3 May 1981; 1♀, 14 km W by N Hope Vale Mission (ex. Berl. 729), 15°16'S 144°59'E, A. Calder & J. Feehan, 7–10 May 1981; 2♀♀, 3♂♂, Mt Windsor Tableland (ex. Berl. 490), 16°18'S 145°05'E, 850 m, RWT, 20 Mar 1975, rf; 1♀, Mt Tiptree (ex. Berl. 1006), 17°03'S 145°37'E, B. Halliday, 13 Jul 1984, rf; 1♀, 3.2km N Atherton (ex. Berl. 275), 17°14'S 145°29'E, J.G. Brooks, 5 May 1970, rf; 2♀♀, Mulgrave R (ex. Berl. 316), 17°15'S 145°46'E, 75 m, RWT & J. Feehan, 19 Jun 1971, rf; 1♀, Barrine NP (ex. Berl. 486), 17°16'S 145°38'E, 760 m, RWT, 21 Mar 1975, rf; 1♀, Eacham NP (ex. Berl. 484), 17°18'S 145°37'E, RWT, 23 Mar 1975, rf; 1♀, 20 km S Ravenshoe (ex. Berl. 358), 17°45'S 145°32'E, 800 m, RWT & J. Feehan, 3 Jul 1971, rf; 1♀, Paluma (ex. Berl. 207), 19°00'S 146°12'E, 810 m, E. Britton, 18 Jan 1970, rf; 3♀♀, 4♂♂, c. 3 km S Eungella (ex. Berl. 487, 488), 21°09'S 148°29'E, 780 m, RWT, 26 Mar 1975, rf; 1♀, 16 km N Eungella (ex. Berl. 493), 21°03'S 148°35'E, RWT, 13 Sep 1975.

Distribution. Queensland: throughout Wet Tropics, south to Eungella, north to Mt Tozer, Cape York Peninsula (Fig. 1), mostly in rainforest, 75–1200 m, mostly above 650 m.

Description. Length up to 24 mm; width of head shield up to 2.85 mm. Colour (based on specimens in absolute ethanol): antenna yellow to pale orange with several dark pigment spots occasionally present on dorsal side of articles in proximal third of antenna; head shield yellow with brown mottled network; tergites pale yellow to pale orange with dark (sometimes tinged with purple) mottling concentrated in longitudinal median band and near margins; dark pigment spots often present near tergal margins; maxillipedes pale orange; sternites pale yellow to pale orange with some faint purple mottling around margins; prefemur to tibia pale to moderate yellow with purple mottling, tarsi a slightly deeper orange; genital sternite and gonopods yellow.

Head shield smooth. Frontal margin with strong median notch; posterior margin transverse or weakly concave; border slightly wider posterolaterally than medially. Median furrow incised for about 1/6 length to transverse suture, shallow throughout. Antennal length 4.1–5.7 times width of head shield, usually extending back to tergite 5 (Fig. 7A); 33–40 articles, majority of specimens examined with 36; basal two articles much larger than succeeding two; relatively gradual change in length of articles along rest of antenna (Fig. 10G,H), articles 3 to 8–10 typically wider than long, gradually elongating along antenna with more

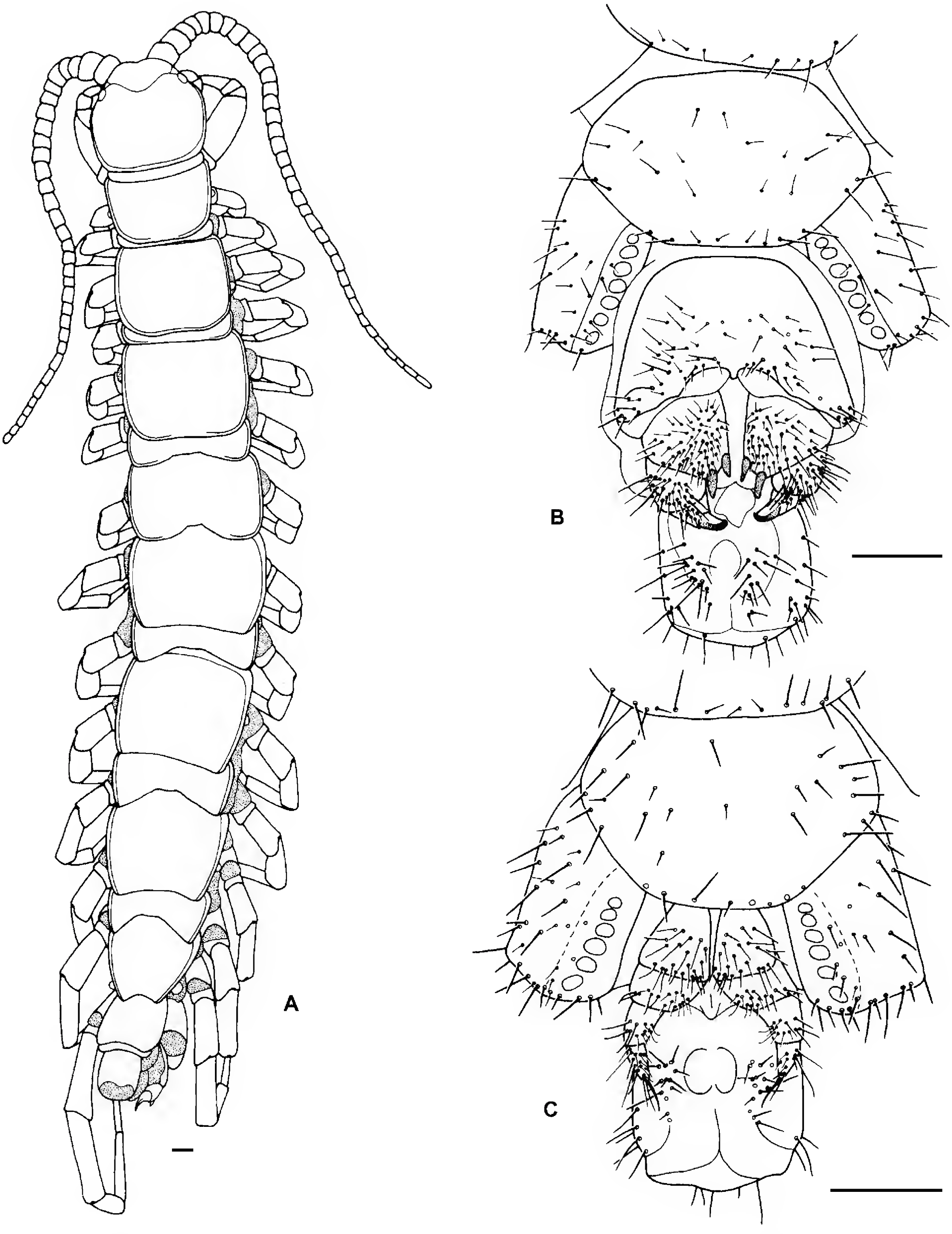

Fig. 7. *Henicops tropicanus* n.sp. (*A*) holotype, ♀ QM S39941, 12km WNW Mossman, QLD. (*B*) ♀ QM S39911, terminal segments and gonopods, Mossman Bluff camp, W Mossman, QLD. (*C*) ♂ QM S39925, terminal segments and gonopods, Mt Hartley, QLD. Scales 0.5 mm.

distal articles up to twice as long as wide (Fig. 10I); gradational increase in density of setae to about tenth article, then more or less constant. Ocellus moderately large, overhanging lateral margin of head (Fig. 9A), usually translucent, sometimes whitish to dark purple, domed. Tömösváry organ small, deep, longitudinally elliptical, outer edge at anterolateral margin of cephalic pleurite (Fig. 9D–F).

Small transverse seta projects medially from pit in labral sidepiece (Fig. 9C). Labral margin with rounded shoulder beside midpiece, with pronounced break in curvature where branching bristles overhang margin; fringe composed of up to 30 densely grouped bristles with many short, spine-like projections along their length, a few longer spines at distal end (Fig. 9G).

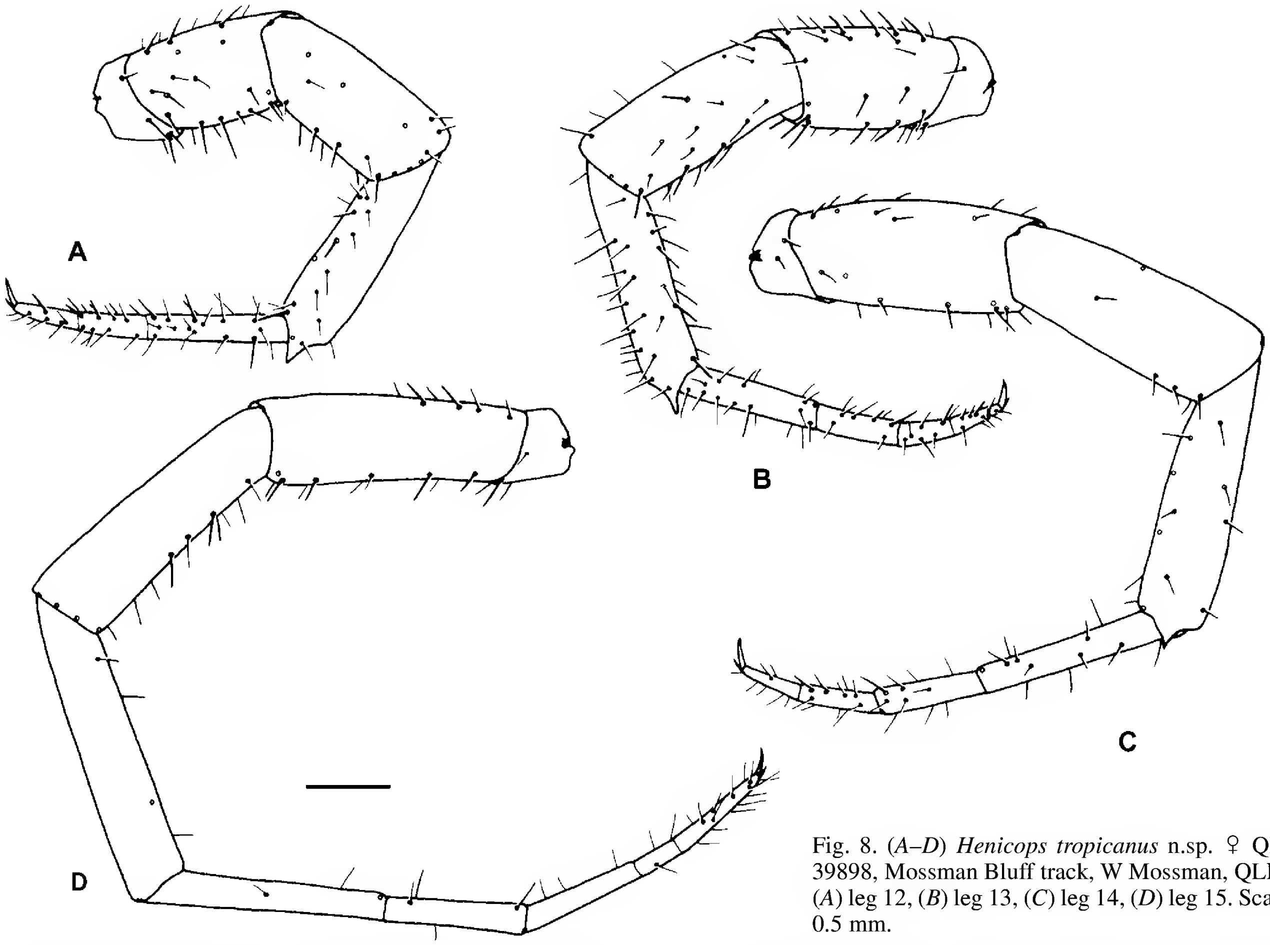

Fig. 8. (*A–D*) *Henicops tropicanus* n.sp. ♀ QM 39898, Mossman Bluff track, W Mossman, QLD: (*A*) leg 12, (*B*) leg 13, (*C*) leg 14, (*D*) leg 15. Scale 0.5 mm.

Maxillipede coxosternum trapezoidal to subsemicircular, dental margin broad, each half weakly convex (Fig. 9H–K); median notch lacking; teeth moderately large, triangular projections, invariably 3+3, usually with a slightly wider space between the outer tooth and middle tooth (Fig. 9K) but ranging from equidistant to space between outer and middle tooth nearly twice that between inner and middle tooth. Coxosternum bearing moderate number of large, scattered setae, usually with distinctly denser setation behind dental margin and anterolaterally (Fig. 9I,K). Tarsungulum with long, slender pretarsal section, as much as twice length of tarsal section (Fig. 9H,L). Setae on telopodite somewhat more abundant on inner part of femur, tibia and tarsal section of tarsungulum than on outer part, these setae moderately long.

Mandible: Four paired teeth on right mandible, left with smaller flattened fifth tooth adjacent to furry pad (Fig. 10A,B). Approximately 20 aciculae differentiated into two rows (Fig. 10C,D); aciculae in dorsal part of outer row with pronounced serrations on both margins along distal half, those in ventral part of outer row with a simple margin or with weak scalloping distally; aciculae of inner row with simple margin (Fig. 10C,D). Fringe of branching bristles skirts aciculae, with transition to rows of scales with multifurcating spine fringes adjacent to midpoint of the second most ventral tooth; scales gradually shortening dorsally (Fig. 10F) to terminate before reaching furry pad (Fig. 10K); ventralmost bristles in fringe narrow-based, lacking spine-like projections on basal sixth to eighth of bristle, spine-like projections abundant and even along remainder of bristle (Fig. 10E); bristles branching into a few spines distally. Accessory denticle field without grooves between rows of denticles or at margin of denticle field (Fig. 10A,F); largest accessory denticles bluntly conical, grading into smaller triangular denticles then small elongate rods near fringe of scale-like bristles; band of unsculpted cuticle on dorsalmost tooth separates accessory denticles from furry pad; furry pad with many elongate, simple bristles (Fig. 10K), some bristles with bifid terminations.

First maxilla: Minute wedge-shaped sternite (Fig. 10L). Coxal process trapezoidal, with a few plumose setae and up to 10 simple setae on anteromedial edge (Fig. 10J), this cluster slightly separated from a few simple setae on inner edge of coxal process; plumose setae with numerous short, spine-like branches along their distal third. Cluster of about six barb-like sensilla microtrichoidea on posterolateral part of coxal process (Fig. 10J). Distal article of telopodite with two rows of about 15 plumose setae along inner margin; branches developed along distal half of these setae (Fig. 10M); shorter simple setae on membranous strip alongside inner margin; main field of distal article of telopodite bearing a few setae anteriorly.

Second maxilla: Sternite small, fused with coxae. Band of 8–11 short setae along anterior part of coxa. Tarsus bearing numerous simple setae on outer surface, cluster of many plumose setae on membranous patch on inner surface (Fig. 11D,E); branches on plumose setae mostly confined to distal half. Claw small, composed of five digits, median digit long, thick, with shorter, slender digit between median and each outer digit (Fig. 11E).

Tergites weakly wrinkled. T1 generally trapeziform, smaller than T3, slightly narrower than head shield (Fig. 7A), about 70% width of widest tergite (T8), posterior

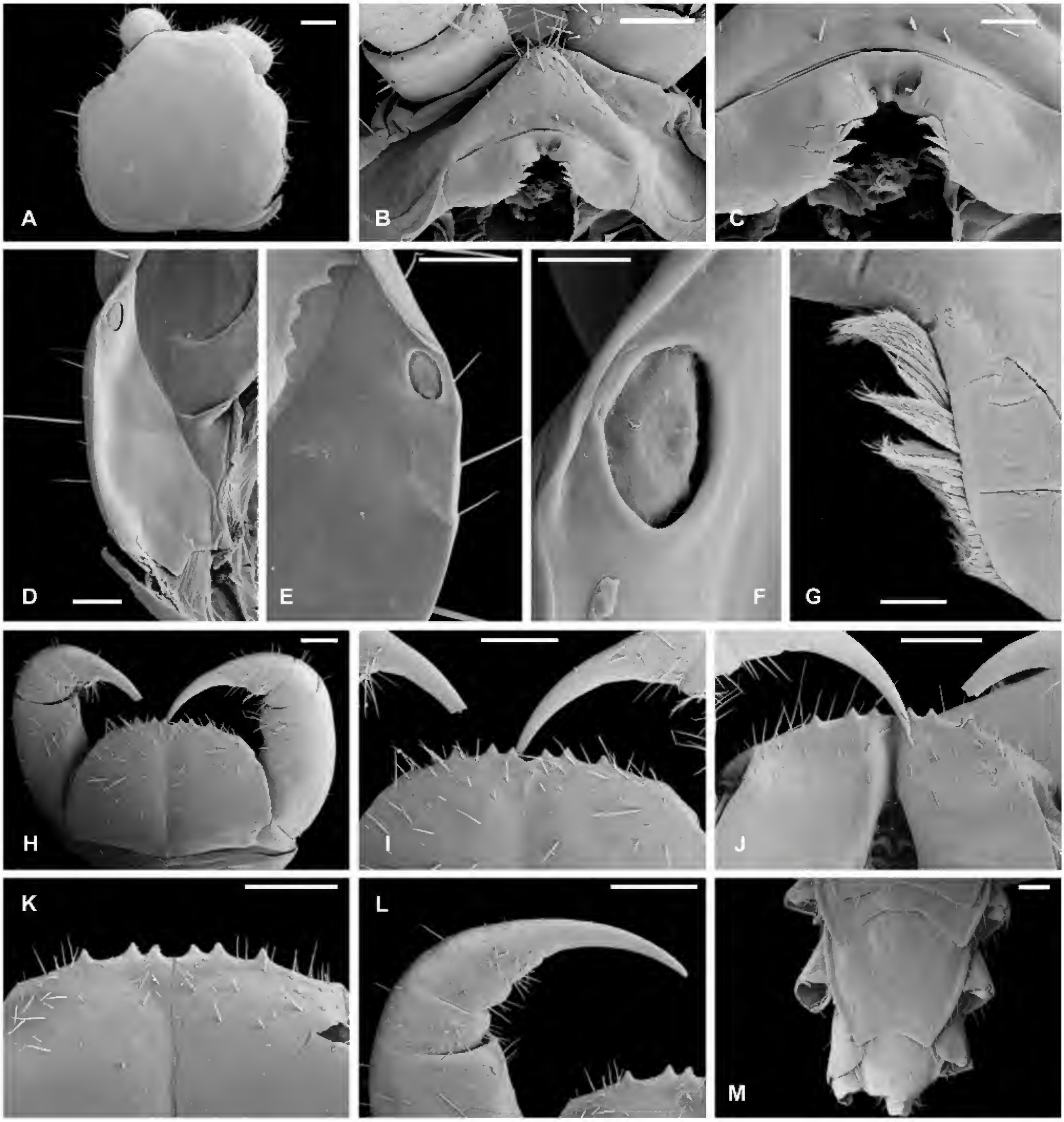

Fig. 9. *Henicops tropicanus* n.sp. (*A,E,K–M*) ♂ AM KS83631, Eungella NP, QLD: (*A*) dorsal view of head shield, scale 300 µm; (*E*) cephalic pleurite, scale 100 µm; (*K*) ventral view of maxillipede dental margin, scale 300 µm; (*L*) telopodite of maxillipede, scale 300 µm; (*M*) dorsal view of posterior tergites, scale 300 µm. (*B–D,F–J*) ♂ QM S39898, Mossman Bluff track, QLD: (*B*) ventral view of head, scale 300 µm; (*C*) clypeus and labrum, scale 100 µm; (*D*) cephalic pleurite, scale 100 µm; (*F*) Tömösváry organ, scale 30 µm; (*G*) labral margin, scale 30 µm; (*H*) ventral view of maxillipede, scale 300 µm; (*I,J*) ventral and dorsal views of maxillipede dental margin, scales 300 µm.

angles rounded, posterior margin transverse; lateral margins subparallel in T3, slightly convex in T5, posterior angles rounded in both, posterior margin faintly concave in TT3 and 5; TT1 and 3 bordered posteriorly; borders of TT5 and 7 incomplete posteriorly; posterior margin of T7 with transverse or convex medial sector, having independent curvature from lateral sectors, posterior angles gently triangular, rounded; lateral margins of TT4–14 convex, all bordered laterally; posterior margin of T8 weakly concave, posterior angle blunt, TT10 and 12 posterior margins gently concave, posterior angles with obtuse, blunt corners; TT6, 9, 11 and 13 embayed with transverse posteromedial third, posterior angle of T6 rounded, T9 blunt, TT11 and 13 with sharp triangular projections; posterior margin of T14 concave, with blunt posterior angles.

Short to moderate, slender setae along lateral borders of all tergites, often with 3–5 longer, thicker setae concentrated on anterolateral border; often cluster of several short setae

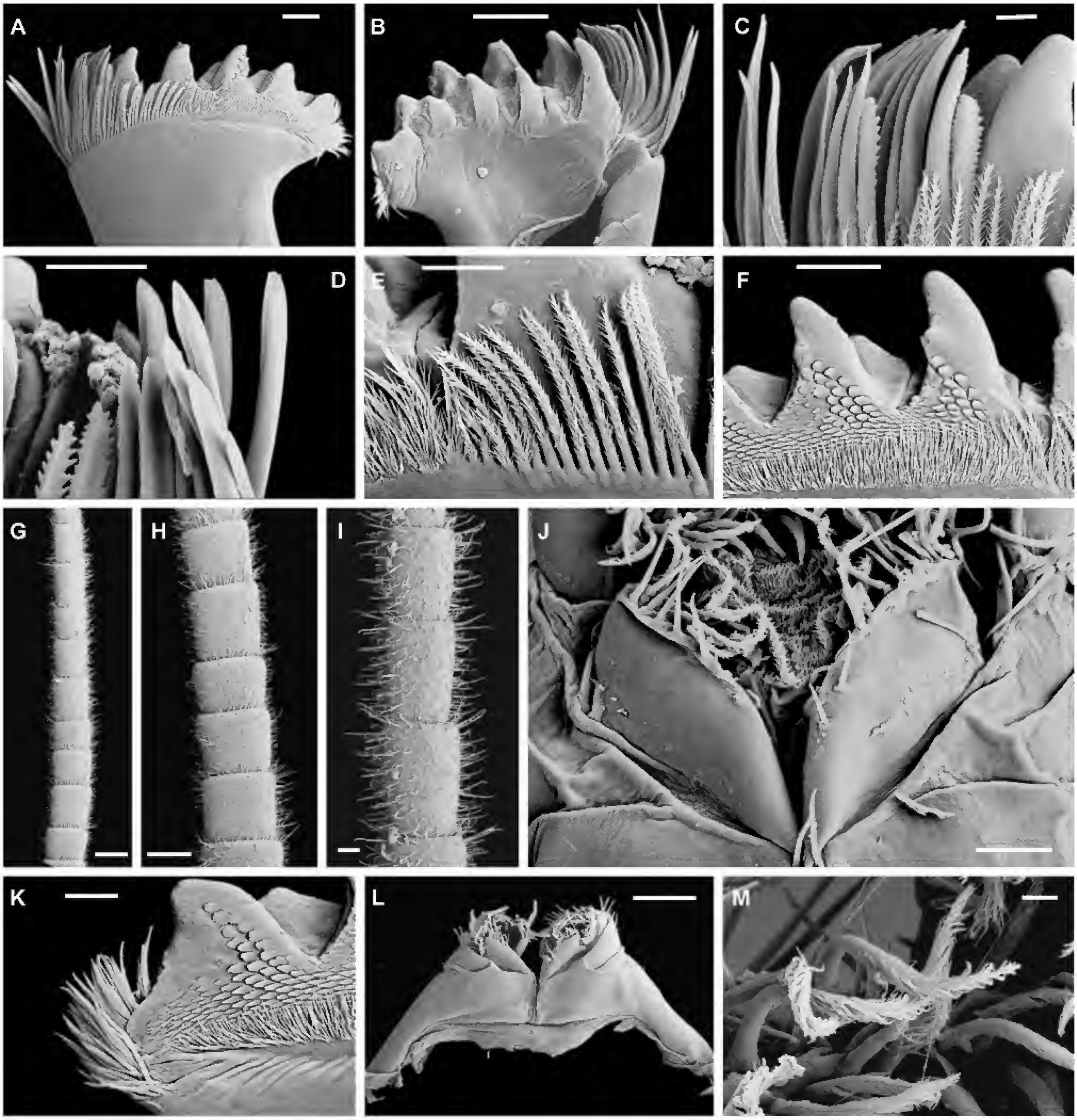

Fig. 10. *Henicops tropicanus* n.sp. (*A–C,G–H,J,M*) ♂ QM S39898, Mossman Bluff track, QLD: (*A,B*) outer (anterior) and inner (posterior) views of gnathal edge of left mandible, scale 50 µm; (*C*) mandibular aciculae, scale 15 µm; (*G,H*) antennal articles, scales 200 µm, 150 µm; (*J*) coxal processes of first maxillae, scale 50 µm; (*M*) plumose setae on inner margin of first maxillary telopodite, scale 10 µm. (*D–F,K*) ♀ QM S39898, right mandible: (*D*) aciculae, scale 30 µm; (*E*) fringe of branching bristles, scale 30 µm; (*F*) teeth, showing accessory denticles, and fringe of branching bristles, scale 50 µm; (*K*) dorsal tooth and furry pad, scale 30 µm. (*I,L*) ♂ AM KS83631, Eungella NP, QLD: (*I*) antennal articles, scale 100 µm; (*L*) first maxillae, scale 150 µm.

on posterior angles of tergites; few short, slender setae scattered sparsely over surface of most tergites. A few moderate to long setae on margins of sternites, 1–3 setae at anterolateral corner most prominent anteriorly in trunk; setae along posterolateral and posterior margins more prominent in posterior segments; posterior margin fringed by 6–10 setae on sternites 13–15; consistently strong pair of setae on anteromedial part of sternites.

Legs: Strong, pointed distal projections with sclerotized tips on tibiae of legs 1–14. Prefemur of legs 1–13 with short to moderate setae scattered on anterior and posterior faces, some longer, thicker setae on ventral edge of prefemur, femur and tibia; longest setae on femur and tibia equal to (Fig. 8B) or shorter than (Fig. 8A) longest on prefemur; a few thickened setae encircling distal margin of femur; strong, pigmented seta at ventrodistal end of tibia on anterior face of legs 1–13; tarsus with combination of slender setae of fairly even length, and four pairs of thicker, divergent, pigmented setae on ventral side of legs 1–13 (Fig. 11K), two of these just proximal to articulations between tarsomeres, one near midlength of distal tarsomere. Setae on legs 14 and 15 more uniformly slender and sparsely

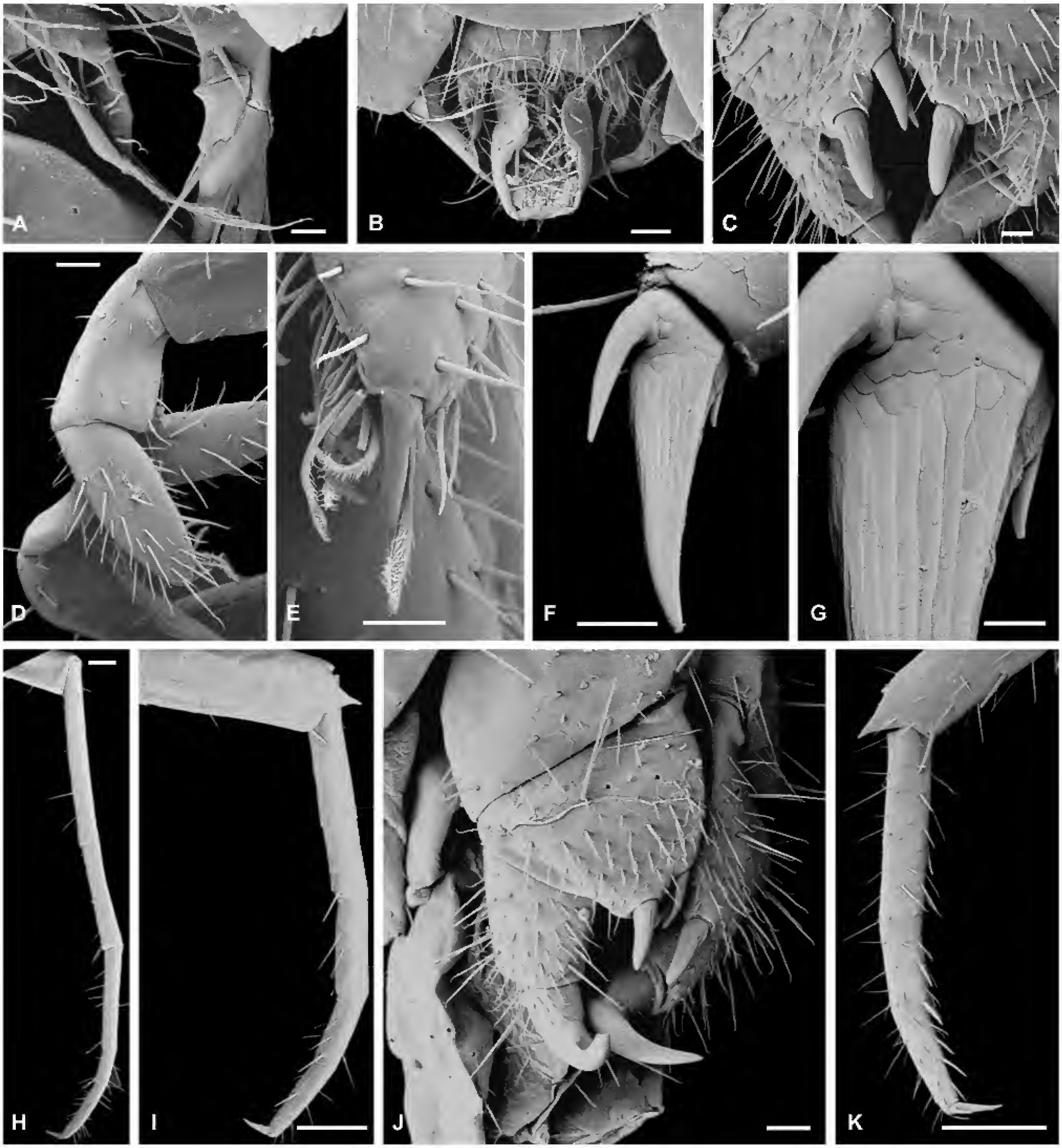

Fig. 11. *Henicops tropicanus* n.sp. (*A,B,F,G,K*) ♂ AM KS83631, Eungella NP, QLD: (*A*) terminal process of ♂ gonopod, scale 30 µm; (*B*) ventral view of terminal segments and gonopods, scale 100 µm; (*F,G*) anteroventral views of pretarsus of leg 14, scales 30 µm, 10 µm; (*K*) tibia, tarsus and pretarsus of leg 12, scale 100 µm. (*C,H,J*) ♀ QM S39898, Mossman Bluff track, QLD: (*C*) gonopods, scale 50 µm; (*H*) tarsus and pretarsus of leg 15, scale 300 µm; (*J*) ventrolateral view of gonopods, scale 100 µm. (*D,E,I*) ♂ QM S39898, Mossman Bluff track, QLD: (*D,E*) distal part and claw of second maxilla, scales 100 µm, 50 µm; (*I*) tibia, tarsus and pretarsus of leg 13, scale 300 µm.

distributed than on preceding legs, especially sparse on tibia and basitarsus of leg 15. Three tarsomeres in legs 1–12 (Fig. 8A), with divided basitarsus. Condyle at joint between basitarsus and distitarsus on legs 13–15 only. Four tarsomeres in legs 13 and 14, basitarsus and distitarsus with two parts each (Figs. 8B,C, 11I); proximal tarsomere nearly 70% length of basitarsus and 55–60% length of distitarsus on leg 14. Leg 15 with five tarsomeres, basitarsus having two, distitarsus three (Figs. 8D, 11H). Distitarsus 70–80% length of basitarsus on leg 15; basitarsus 12–14 times longer than broad; proximal tarsomere 55–65% length of basitarsus; three tarsomeres comprise about 45–50, 15–20 and 30–40% (proximal to distal) length of distitarsus. Pretarsal claws (Fig. 11F,G) as described below for *H. milledgei*.

Coxal pores round or ovate (Fig. 7B,C), commonly 5,6,6,6/5,6,6,6 in large males and females, males maximum 5,6,6,6/5,6,6,6, minimum 3,4,4,4/3,4,4,4; females maximum 7,7,7,7/7,7,7,7, minimum 3,4,5,5/3,4,5,5. Coxal pore field set in shallow groove, distal pore(s) partly concealed by anteroventral face of coxa. Anal pores large in both sexes.

Female (Fig. 7B): Sternite of segment 15 transverse or convex posteromedially. Tergites of first genital segment and telson usually well sclerotized. Sternite of first genital segment large, posterior margin concave between condyles of gonopods except for small median projection, posterior two-thirds fairly evenly scattered with setae of varied length; short setae concentrated in a band along posteromedial margin. First article of gonopod bearing two (three in one specimen) large, bullet-shaped spurs, inner spur slightly smaller than outer; spurs gently curved such that tip points up (Fig. 11C,J); first and second articles of gonopod with mix of many short, moderate and long setae, up to 56 on first article, up to 37 on second; third article with up to 10 setae, mostly moderate, one or two long ones (Fig. 11J). Claw large, undivided.

Male (Fig. 7C): Sternite of segment 15 rounded posteriorly. Sternite of first genital segment small, divided, with transverse posterior margin, bearing numerous moderately long setae, short setae concentrated in a band near posterior margin (Fig. 11B). Gonopod of three articles and tapering, seta-like terminal process that bears many short spine-like projections (Fig. 11A), the three articles each bearing numerous short to moderately long setae, typically about 15, 10–12 and 10 for first to third articles, respectively; extended penis approximately equal in length to first article of gonopod.

Larval stadia (identified by correspondence to leg and limb-bud pairs in *Lamyctes emarginatus*: Andersson, 1979, 1984) (ANIC Berl. 1062): Stadium LII with 8 pairs of legs and two pairs of limb-buds; 14 antennal articles. Stadium LIII with 10 pairs of legs and two pairs of limb-buds; 25 antennal articles. Stadium LIII with 12 pairs of legs and three pairs of limb-buds; 25 antennal articles. Stadia LII–IV all with 3+3 teeth on dental margin of maxillipede coxosternum.

Discussion. As discussed above under the *Henicops dentatus* Group, *H. dentatus* and *H. tropicanus* n.sp. share numerous characters distinguishing them from other species of *Henicops*, and they appear to be sister taxa. In spite of their geographic separation, the two species are remarkably similar. They can consistently and most readily be distinguished by the morphology of the female gonopod, in particular the size and shape of the spurs on the basal article. *Henicops dentatus* has two, small bullet-shaped (Fig. 6G) or distally-truncated (Figs. 4F, 6H) spurs, with the outer spur as much as 40% longer and 50% wider than the inner spur. In contrast, the gonopods of *H. tropicanus* (Figs. 7B, 11C) bear spurs that are larger and more elongate (with the outer spur of *H. tropicanus* being approximately 40% the length of the inner margin of the first article of the gonopod, compared to approximately 20% in *H. dentatus*) and both spurs are of more nearly equal size. Though the shape of the spurs varies within *H. dentatus*, they are consistently shorter and stouter than in *H. tropicanus*. In contrast to the distinction made possible by the female gonopods, the male gonopods of the three species of *Henicops* treated herein (Figs. 4C, 7C, 12C) provide no obvious characters for specific distinction.

Two features of the mandibular gnathal edge permit distinction between *Henicops tropicanus* and *H. dentatus*. The Western Australian *H. dentatus* has a narrower fringe of branching bristles on the dorsal part of the mandible (Figs. 5D,I versus 10F), this including the entire row of scale-like bristles. As well, the branching bristles on the ventral part of the fringe have a longer non-spinose (basal) extent (Fig. 5H versus 10E). In both of these characters, the state in *H. tropicanus* is plesiomorphic, being shared with *H. maculatus* (Edgecombe *et al*., 2002: figs. 4A, 5C), *H. milledgei* (Fig. 14H), *H. brevilabiatus* (Fig. 2A,B,D) and outgroups.

Specimens of *Henicops tropicanus* often have a narrower medial sector to "notched" tergites 7, 9 and 11 than does *H. dentatus* (compare Fig. 3 with Fig. 7A) but this difference is inconsistent. Setation of legs 14 and 15 often also serves to distinguish between the two species: *H. tropicanus* typically has fewer setae on legs 14 and 15 (Fig. 8C,D) than *H. dentatus* (Figs. 4C,D), most notably on the tibia and basitarsus of leg 15 (Fig. 11H), and has gracile setae on the prefemur of leg 15 versus sometimes spine-like setae in *H. dentatus*.

Henicops tropicanus normally has two spurs on the female gonopod, only one specimen (QM S38899) having three spurs. Three-spur variants are also exceptional in other members of the Henicopinae. For example, specimens of *Lamyctes mauriesi* Demange, 1981, are recorded as normally having two conical spurs on each gonopod, but single specimens from Tenerife and Gran Canaria have two such spurs on one gonopod and three on the other (Eason & Enghoff, 1992).

Henicops milledgei n.sp.

Figs. 12–16

Etymology. For Graham Milledge, who collected this species throughout most of its range.

Type material. HOLOTYPE: MV NOH-2207, ♀ (Fig. 12A), Strzelecki Ra, Tarra-Bulga NP, VIC, 0.5 km NNE Tarra Valley Picnic Area, 38°26'40"S 146°32'30"E, *Nothofagus cunninghamii* forest, G.A. Milledge, 14 Nov 1995–10 Jan 1996. PARATYPES: NOH-2208, 1♀, 3♂♂, from type locality, 10 Jan–5 Mar 1996; NOH-2209, 1♀, 1♂, type locality, 5 Mar–7 Mar 1995; NOH-2211, 1♀, 1♂, Tarra-Bulga NP, 0.2 km W Tarra Valley Picnic Area, 38°27'S 146°32'E, 14 Sep–14 Nov 1995; NOH-2212, 1♂, same locality, 14 Nov 1995–10 Jan 1996; NOH-2213, 1♂, same locality, 14 Nov 1995–10 Jan 1996; NOH-2214, 1♀, 3♂♂, same locality, 10 Jan–5 Mar 1996; NOH-2215, 1♂, same locality, 7 May–16 Jul 1996; NOH-2220, 1♀, 2♂♂, same locality, 5 Mar–7 May 1996; NOH-2217, 1♀, Tarra-Bulga NP, Bulga Picnic Area, 38°25'30"S 146°34'20"E, 14 Nov 1995–10 Jan 1996; NOH-2218, 1♂, same locality, 10 Jan–5 Mar 1996; NOH-2219, 2♀♀, 1♂, same locality, 5 Mar–7 May 1996.

Other material. VICTORIA: MV: OTWAY RA, leg. G.A. Milledge: NOH-1045, 2♀♀, 1♂, Philips Track, 0.5 km N Triplet Falls, 38°40'S 143°29'E, 6 Sep–15 Nov 1994; NOH-1046, 1♀, 1♂, same locality, 15 Nov 1994–31 Jan 1995; NOH-1047, 3♀♀, same locality, 31 Jan–11 Apr 1995; NOH-1048, 1♂, same locality, 11 Apr–14 Jun 1995; NOH-1049, 1♀, same locality, 14 Jun–29 Aug 1995; NOH-1050, 2♀♀, 2♂♂, Young Creek Rd, 0.4 km NW Triplet Falls, 38°40'S 143°29'E, 6 Sep–15 Nov 1994; NOH-1052, 7♀♀, 3♂♂, same locality, 15 Nov 1994–31 Jan 1995; NOH-1053, 1♀, same locality, 31 Jan–11 Apr 1995; NOH-1054, 3♀♀, same locality, 11 Apr–14 Jun 1995; NOH-1055, 3♀♀, 1♂, Young Creek Rd, 0.2 km NE Ciancio Ck Crossing, 38°40'S 143°29'E, 6 Sep–15 Nov 1994; NOH-1056, 1♀, same locality, 15 Nov 1994–31 Jan 1995; NOH-1058, 2♀♀, 1♂, 31 Jan–11 Apr 1995; NOH-1059, 1♀ (Figs. 14K,L, 15F, 16G–J), 2♂♂, same locality, 11 Apr–4 Jun 1995; NOH-1060, 1♂, Aire Crossing Tk, 0.5 km N Aire R. Crossing, 38°40'S 143°29'E, 6 Sep–15 Nov 1994; NOH-1061, 2♂♂, Beauchamp Falls, 38°39'S 143°36'E, 6 Sep–15 Nov 1994; NOH-1062, 7♀♀, 1♂, same locality, 15 Nov 1994–31 Jan 1995; MV NOH-1063, 8♀♀, 1♂, same locality, 31 Jan–11 Apr 1995.

CENTRAL HIGHLANDS, leg. G.A. Milledge: NOH-1778, 1 larval stadium LII, 2 larval stadia LIII, Cement Creek Reserve, 2.2 km ESE Mt Donna Buang, 37°43'S 144°42'15"E, 13 Dec 1994; NOH-1779, 2♀♀, 1♂ (Figs. 14B,C,H–J, 15B,D,E,G,L,M, 16A,D–F,K,L), same locality, 29 Nov 1994–20 Jan 1995; NOH-1784, 3♀♀, same locality, 21 Jan–7 Apr 1995; MV NOH-1782, 4♀♀ (Fig. 12B), 4♂♂, 1 larval stadium LII, Donna

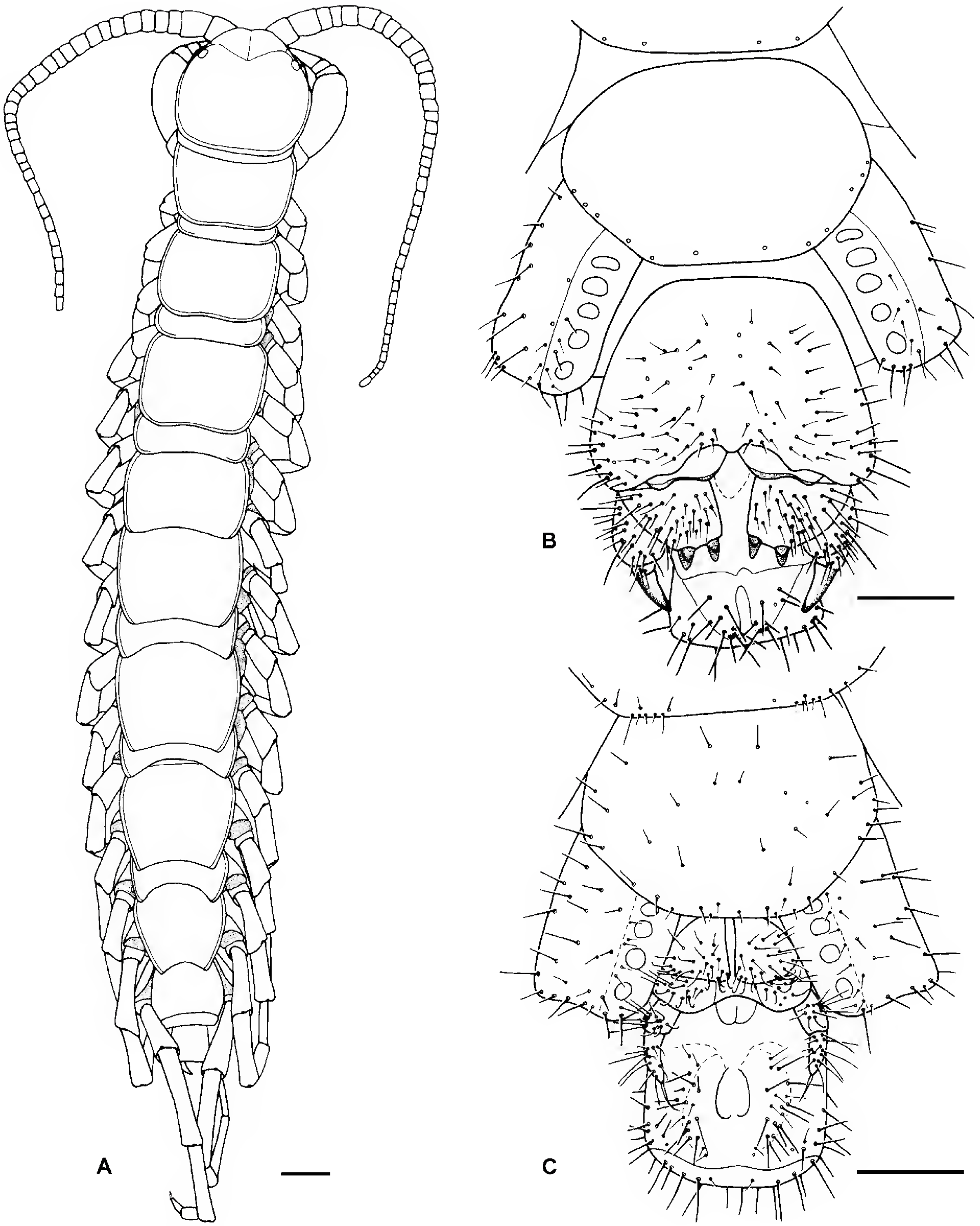

Fig. 12. *Henicops milledgei* n.sp. (*A*) holotype ♀ MV NOH-2207, dorsal view, Tarra-Bulga NP, Strzelecki Ranges, VIC. (*B*) ♀ MV NOH-1782, terminal segments and gonopods, 1km SW Mt Donna Buang, Central Highlands, VIC. (*C*) ♂ MV NOH-1792, terminal segments and gonopods, Acheron Gap, Central Highlands, VIC. Scales 0.5 mm.

Buang Rd, 1 km SW Mt Donna Buang, 37°43'S 144°40'E, 29 Nov 1994–20 Jan 1995; NOH-1783, 6♀♀, 1♂, same locality, 21 Jan–7 Apr 1996; NOH-1786, 2♀♀, 2♂♂, 1 larval stadium LII, Myrtle Gully Reserve, 3.4 km WSW Mt Donna Buang, 37°43'S 144°38'30"E, 29 Nov 1994–20 Jan 1995; NOH-1787, 5♀♀, 3♂♂, same locality, 21 Jan–7 Apr 1995; NOH-1788, 1♀, Road 26, 0.2 km WNW Donna Buang Rd junct., 37°43'S 144°39'30"E, 16 Feb 1995; NOH-1790, 1♀, Acheron Gap, 6 km NE Mt Donna Buang, 37°40'43"S 144°44'20"E, 20 Feb 1996; NOH-1792, 2♂♂ (Fig. 12C), same locality, 26 Oct–28 Dec 1995; NOH-1793, 2♀♀, same locality, 28 Dec 1995; NOH-1794, 4♀♀, same locality, 21 Feb–23 Apr 1996; NOH-1795, 1♀, same locality, 23 Apr–25 Jun 1996; NOH-1796, 2♀♀, 2♂♂, 0.7 km N Acheron Gap, 7 km NE Mt Donna Buang, 37°40'17"S 144°44'20"E, 21 Feb–23 Apr 1996; NOH-1797, 4♂♂, same locality, 28 Dec 1995–21 Feb 1996; NOH-1800, 1 larval stadium LIII, The Big Culvert, 2.5 km ENE Mt Observation, 37°33'36"S 145°52'15"E, 28 Dec 1995.

STRZELECKI RA, leg. G.A. Milledge: NOH-2222, 1 larval stadium LIII, Tarra-Bulga NP, Bulga Picnic Area, 38°25'30"S 146°34'20"E, 7 May–16 Jul 1996; NOH-2225, 1♀ (Fig. 13A–D), 2♂♂, Gunyah-Toora Rd, 2 km SSW Gunyah Gunyah, 38°32'30"S 146°19'E, 14 Nov 1995–10 Jan

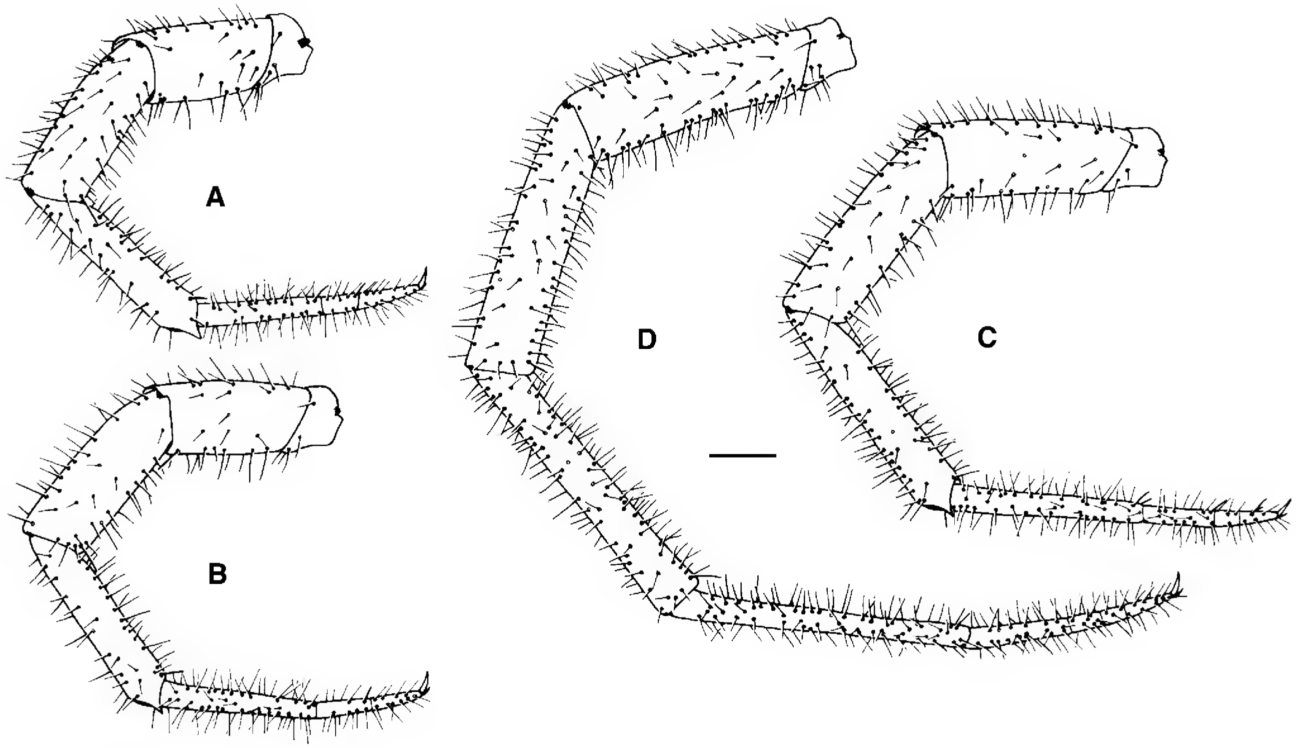

Fig. 13. *Henicops milledgei* n.sp. ♀ MV NOH-2225, Mt Donna Buang, Strzelecki Ranges, VIC: (*A*) leg 12, (*B*) leg 13, (*C*) leg 14, (*D*) leg 15. Scale 0.5 mm.

1996; NOH-2227, 1♀, Jeeralang West Rd, 0.1 km N Binns Hill Junction, 38°26'30"S 146°29'E, 10 Jan–5 Mar 1996.

AUSTRALIAN MUSEUM: KS35864, 1♀, Otway Ra, 38°27'S 143°58'E, A. Frazer, Aug 1979; KS35869, 1♂, Otway Ra, Lavers Hill, 38°41'S 143°24'E, A. Frazer, 24 Feb 1979; KS83632, 1♀, Otway NP, Sandy Ridge, Spur Road, 38°46.12'S 143°32.9'E, 278 m, G. Cassis *et al.*, 9 Nov 2002; KS83633, 2♀♀ (Figs. 14A,D–G, 15A,C,H,K, 16B,C), Grampians NP, Wonderland Range, Silverband Rd, 1.2 km S Rosea Campground, 37°10'28"S 142°30'29"E, G.D. Edgecombe & Z. Johanson, 15 Feb 2000, fern gully.

Distribution. Victoria: Otway Ranges, Strzelecki Ranges, Central Highlands, mostly from *Nothofagus cunninghamii* forest; Grampians, sclerophyll forest (Fig. 1).

Diagnosis. *Henicops* with 36–43 (most commonly 40 or 41) antennal articles. Uneven change in length of articles in proximal part of antenna, with short paired articles interspersed between longer articles; T7 with rounded, concave margin; Tömösváry organ small and weak, centrally located on cephalic pleurite; groove in accessory denticle field pronounced on mandibular teeth; female gonopod with two moderately large, bullet-shaped spurs (shared with *H. maculatus*). Mandibular aciculae differentiated into outer row with serrated margins and inner row with mostly simple margins; branching bristles of mandible with sparse spine-like branches on basal part of bristle (shared with *H. dentatus* Group). Uniquely: 3+3 moderate sized teeth on maxillipede coxosternum, with space between outer and middle teeth invariably more than twice the space between inner two teeth; three tarsomeres in leg 13, four in leg 14, five in leg 15, basitarsus undivided in legs 13–15; proximal coxal pores elliptical, distal pores round.

Description. Length up to 28 mm; width of head shield up to 3.3 mm. Colour (based on specimens in absolute ethanol): antenna dark orange, with dark pigment spots usually present, especially on dorsal side and proximally but also common on ventral side of antenna and more distally; head shield dark orange with chestnut mottled network; tergites dark orange with dark mottling covering most of tergite, concentrated in longitudinal median band and near margins, and dark pigment spots concentrated on margins; maxillipedes orange; sternites pale orange with purple mottling around margins, becoming more concentrated in the three posterior sternites; prefemur to tibia pale to moderate yellow with purple mottling; tarsi pale to moderate yellow; genital sternite and gonopods orange with faint purple mottling on genital sternite.

Head shield smooth. Frontal margin with strong median notch and short median furrow; posterior margin transverse; border very slightly wider posterolaterally than posteromedially. Antennal length 3.1–4.7 times width of head shield, usually extending back to tergite 5 (Fig. 12A); 36–43 articles, commonly 40 or 41; basal two articles much larger than succeeding two (Fig. 14A); antenna with a markedly uneven change in the length of articles in proximal part, with short paired articles interspersed between longer articles (Fig. 14B); articles mostly substantially longer than wide in distal half of antenna; antenna densely setose along most of length, with many short, curved sensilla interspersed with long trichoid sensilla (Fig. 14C). Ocellus moderately large, overhanging lateral margin of head, usually translucent, whitish to dark purple, domed. Tömösváry organ small, fairly shallow, longitudinally elliptical, situated inward of anterolateral margin of cephalic pleurite (Fig. 15D,E).

Clypeus with transverse band of six setae medially just in front of labrum (Fig. 15B), cluster of 10 setae at clypeal apex (Fig. 15A). Labral margin with rounded shoulder beside midpiece, with gradual break in curvature where fringe of branching bristles overhangs margin (Fig. 15B); most bristles with short, spine-like projections along their length, some branching into long, slender spines distally (Fig. 15C).

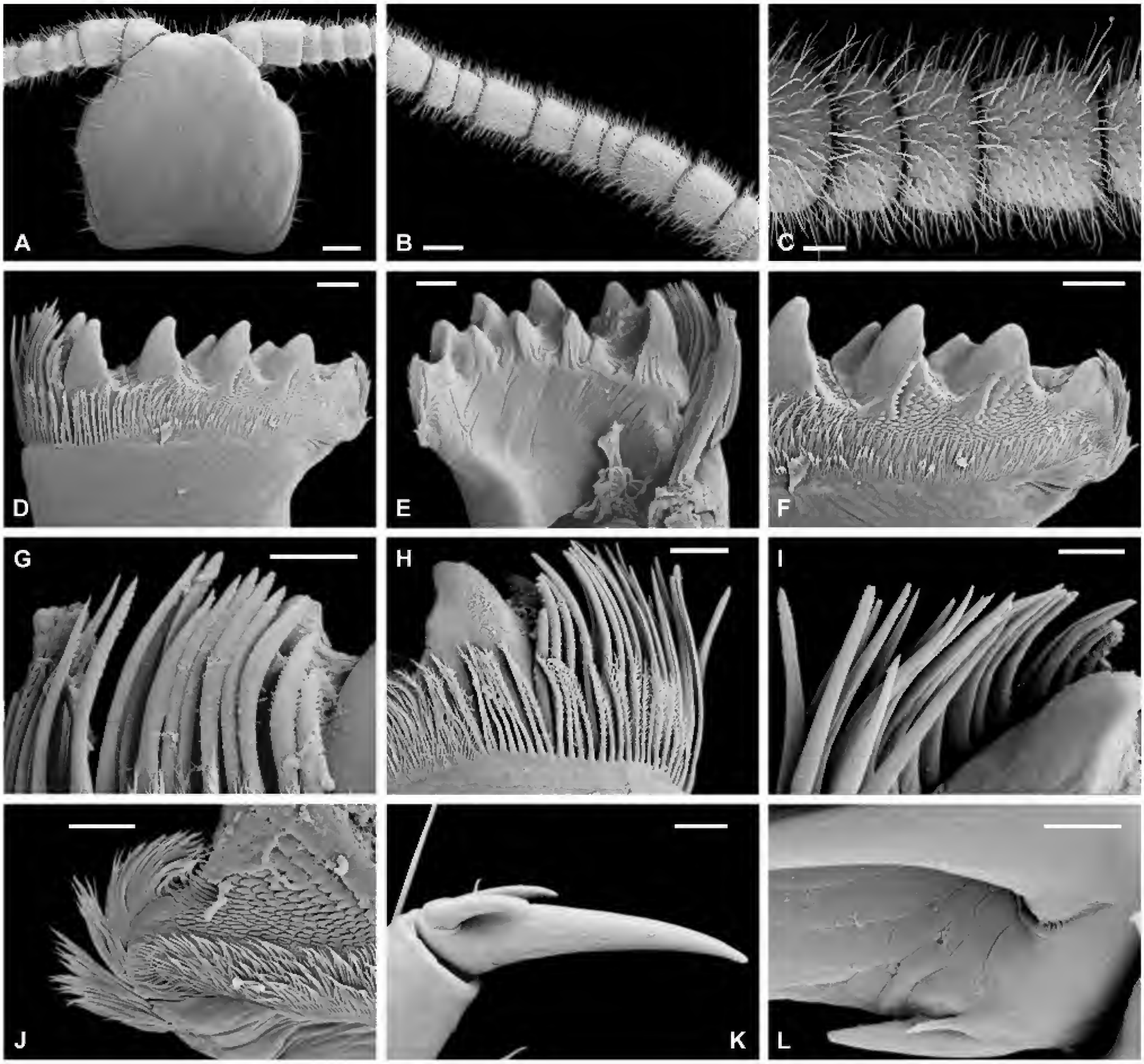

Fig. 14. *Henicops milledgei* n.sp. (*A,D–G*) ♀ AM KS83633, Grampians NP, VIC: (*A*) dorsal view of head shield, scale 100 µm; (*D,E*) outer (anterior) and inner (posterior) views of gnathal edge of left mandible, scales 10 µm; (*F*) mandibular teeth, scale 10 µm; (*G*) aciculae, scale 30 µm. (*B,C,H–J*) ♂ MV NOH-1779, Cement Creek Reserve, Central Highlands, VIC: (*B,C*) antennal articles, scales 30 µm, 10 µm; (*H*) aciculae and fringe of branching bristles of mandible, scale 50 µm; (*I*) inner (posterior) view of mandibular aciculae, scale 30 µm; (*J*) accessory denticles and furry pad of mandible, scale 30 µm. (*K,L*) ♀ MV NOH-1059, Otway Range, VIC: (*K*) anterior view of pretarsus of leg 12, scale 30 µm; (*L*) posterior view of pretarsus of leg 12, scale 10 µm.

Maxillipede coxosternum trapezoidal to subsemicircular, dental margin broad, each half gently convex (Fig. 16A,B); median notch at most narrow, shallow (Fig. 16D); teeth small, triangular projections, invariably 3+3, with space between outer tooth and adjacent tooth more than twice space between inner two teeth (Fig. 16C–E), inner tooth smaller than the others. Coxosternum bearing moderate number of small to moderate sized setae (Fig. 16D), mostly confined to anterior half of coxosternum (Fig. 16A,B). Tarsungulum with long, slender pretarsal section (Fig. 16A,B). Setae on telopodite denser on inner part of femur, tibia and tarsal section of tarsungulum than on outer part, especially long on tarsungulum (Fig. 16C).

Mandible as described for *H. tropicanus* except for the following: ventral aciculae in outer row of aciculae with both margins serrated along their distal fifth to third (Fig. 14G,I); grooved ridge on accessory denticle field of all but ventralmost paired tooth (Fig. 14D,F); ventral bristles in fringe of branching bristles lacking spine-like projections on basal fifth of bristles (Fig. 14H); fringe of scale-like branching bristles extends to furry pad (Fig. 14J); bristles of furry pad curved towards dorsalmost tooth (Fig. 14F,J).

First maxilla (Fig. 15H–J) as described for *H. tropicanus* except: coxal process with a few short simple setae, several laciniate and plumose setae with intermediates between these (some with a few terminal spines, others with numerous short, slender projections along their distal halves) (Fig. 15J); distal article of telopodite with several simple setae scattered over its main field (Fig. 15I). Second maxilla (Fig. 15K–M) as described for *H. tropicanus*.

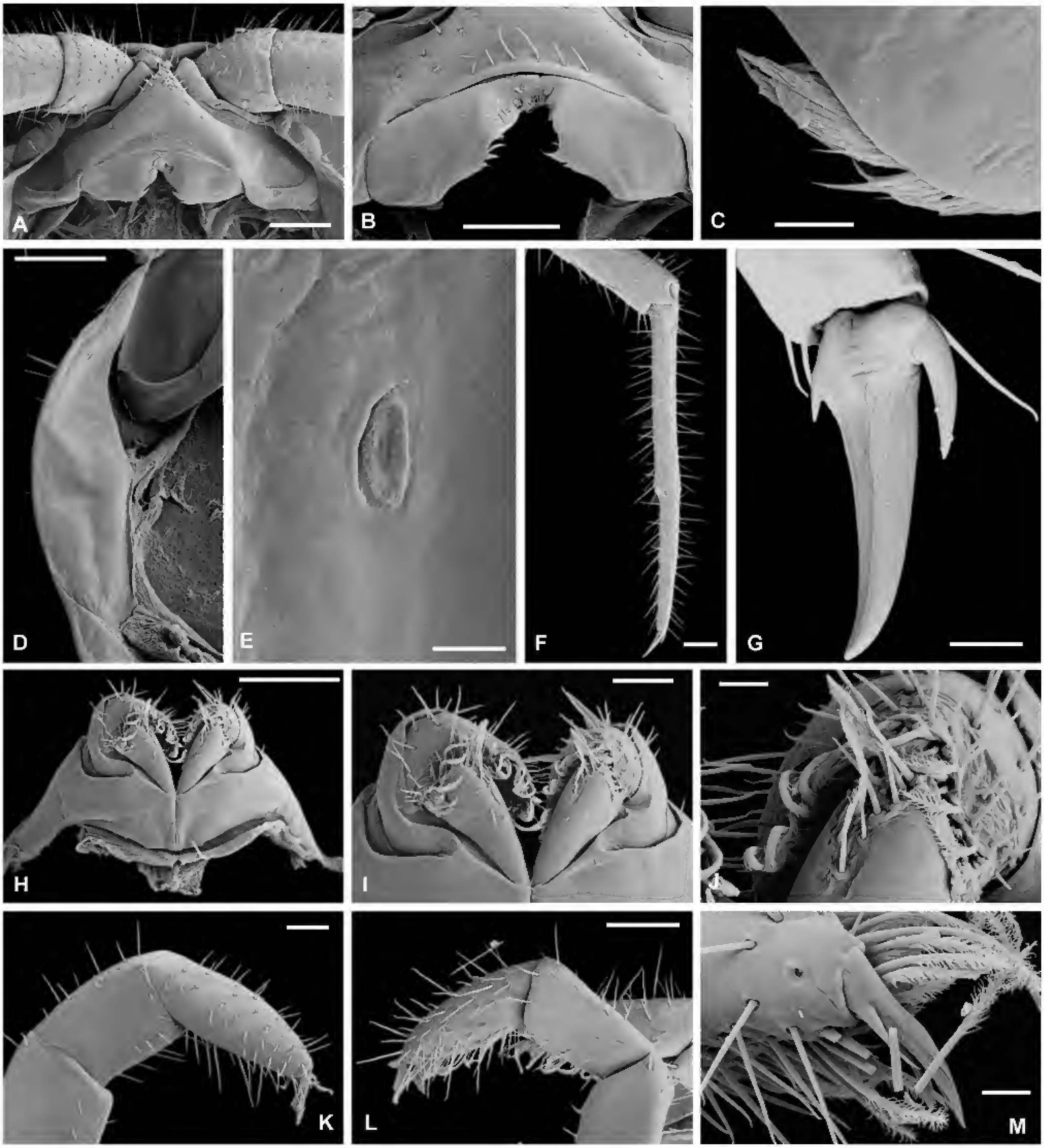

Fig. 15. *Henicops milledgei* n.sp. (*A,C,H–K*) ♀ AM KS83633, Grampians NP, VIC: (*A*) ventral view of head, scale 300 µm; (*C*) labral margin, scale 30 µm; (*H*) first maxillae, scale 300 µm; (*I*) coxal processes and telopodites of first maxillae, scale 100 µm; (*J*) setae on coxal process of first maxilla, scale 30 µm; (*K*) distal part of telopodite of second maxilla, scale 100 µm. (*B,D,E,G,L,M*) ♂ MV NOH-1779, Cement Creek Reserve, Central Highlands, VIC: (*B*) clypeus and labrum, scale 300 µm; (*D*) cephalic pleurite, scale 300 µm; (*E*) Tömösváry organ, scale 30 µm; (*G*) ventral view of pretarsus of leg 15, scale 100 µm; (*L*) distal part of telopodite of second maxilla, scale 200 µm; (*M*) tarsus and claw of second maxilla, scale 30 µm. (*F*) ♀ MV NOH-1059, Otway Range, VIC. Tibia, tarsus and pretarsus of leg 13, scale 300 µm.

Tergites wrinkled, faintly so anteriorly but considerably so in posterior half of trunk. T1 trapeziform, about as wide as head shield (Fig. 12A), about 80% width of widest tergite (T8), posterior angles rounded and posterior margin gently concave; lateral borders subparallel in TT3 and 5, posterior angles rounded, posterior margins gently concave; TT1, 3 and 5 bordered posteriorly; border of T7 incomplete posteriorly; posterior margin of T7 evenly concave, posterior angle blunt; posterior margins of TT8 moderately, fairly evenly concave, posterior angles obtuse, blunt; posterior margins of TT6, 11 and 13 all evenly concave, increasingly so more posteriorly; T9 variably with nearly transverse median sector; posterior angle of T6 rounded, TT9, 11 and 13 with triangular projections; posterior margin of T14

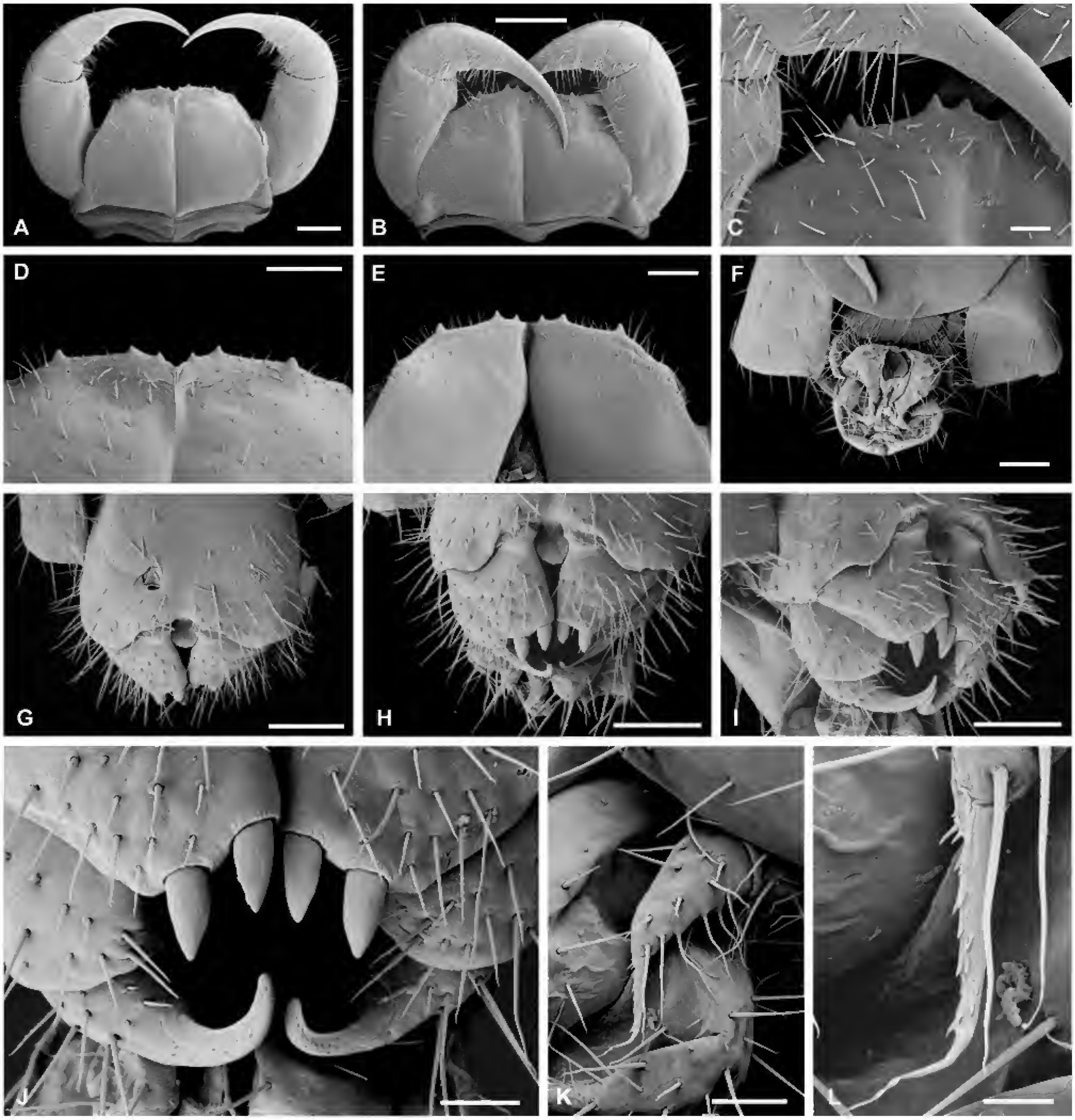

Fig. 16. *Henicops milledgei* n.sp. (*A,D–F,K,L*) ♂ MV NOH-1779, Cement Creek Reserve, Central Highlands, VIC: (*A*) ventral view of maxillipede, scale 500 µm; (*D*) ventral view of dental margin of maxillipede coxosternum, scale 300 µm; (*E*) dorsal view of dental margin of maxillipede coxosternum, scale 300 µm; (*F*) ventral view of terminal segments and gonopods, scale 300 µm; (*K*) distal end of gonopod, scale 100 µm; (*L*) terminal process of gonopod, scale 30 µm. (*B,C*) ♀ AM KS83633, Grampians NP: (*B*) ventral view of maxillipede, scale 500 µm; (*C*) setation of telopodite and dental margin of maxillipede, scale 100 µm. (*G–J*) ♀ MV NOH-1059, Otway Range, VIC: (*G*) ventral view of sternite of first genital segment and gonopods, scale 300 µm; (*H,I*) ventral and ventrolateral views of sternite of first genital segment and gonopods, scales 300 µm; (*J*) gonopods, scale 100 µm.

moderately concave, with obtuse posterior angles; tergite of intermediate segment with weakly concave posterior margin in female, moderately concave margin in male. Tergal surface and margins scattered with short setae, in some specimens relatively numerous, e.g., posterior margins of TT3 and 4 fringed by about 20 setae. Longitudinal median furrow confined to anterior part of sternites, not more than one-third length of sternite.

Legs: Distal spinose projections on tibiae strong, pointed on legs 1–14. Setae relatively uniformly distributed along length of legs, with similar setal density on inner and outer faces of all podomeres; legs 14 and 15 (Fig. 13C,D) with similar setal density as 1–13 (Fig. 13A,B). Three tarsomeres in legs 1–12 (Fig. 13A), with divided basitarsus; tarsal articulations discontinuous on dorsal side of leg in anterior part of trunk; three pairs of consistently strong, pigmented, divergent setae on tarsi of legs 1–12, one just proximal to each articulation between tarsomeres, one near midlength of distal tarsomere. Basitarsus-distitarsus joint with a condyle in legs 13–15 only, basitarsus undivided in these three legs; three tarsomeres in leg 13 (Figs. 13B, 15F); four tarsomeres in leg 14 (Fig. 13C), distitarsus about 65% length of basitarsus, three tarsomeres comprise about 45–55, 15–25 and 25–35% (proximal to distal) length of distitarsus; five tarsomeres in leg 15, the proximal distitarsal podomere about 50–55% length of distitarsus, second and third shorter than fourth (Fig. 13D). Distitarsus 70–85% length of basitarsus in leg 15; basitarsus 10–12 times longer than broad. Pretarsus with anterior and posterior accessory claws on all legs, about 30% length of main claw, inserted on dorsolateral side of main claw, with gentle dorsoventral curvature (Fig. 14K). Main claw gently curved, divided into many elongate, scales along most of its length, with short, polygonal scales ventrolaterally in region beneath proximal part of accessory claws, a few pores between these scales (Fig. 14L), pore openings in the middle of small polygons; scales weakly defined proximally beneath bases of accessory claws and on proximoventral surface of main claw, well defined dorsoproximally. Posteroventral spine ('sensory spur' of Eason, 1964: fig. 486) present on legs 1–14 (Fig. 14L), absent on leg 15 (Fig. 15G), about 15% length of main claw, directed distally, bearing slender subsidiary spine that parallels it on its dorsoproximal half (Fig. 14L); accessory claws and posteroventral spine with surface ornament of linear grooves and ridges.

Coxal pores round, transversely ovate, or elliptical, typically with round distal pores and elliptical proximal pores (Fig. 12B); overwhelmingly 6,5,5,5/6,5,5,5 in large females (width head shield >1.75 mm), 5,4,4,4/5,4,4,4 in large males; maximum in males 5,5,5,5/5,5,5,5. Coxal pore field set in shallow groove. Anal pores large in both sexes.

Female (Fig. 12B): Sternite of segment 15 transverse or convex posteromedially, with about a dozen setae along posterolateral and posteromedial margins. Tergites of first genital segment and telson usually well sclerotized; sternite of first genital segment large, posterior margin concave, with median bulge, between condyles of gonopods, surface scattered with setae, longest and densest posterolaterally (Fig. 16G). First article of gonopod bearing two moderately large, bullet-shaped spurs, inner spur slightly smaller (Fig. 16G–J); spurs gently curved such that tip points up (Fig. 16I); first article usually bearing more than 30 setae in large specimens (up to 38), second article with 12–20 moderately long setae; third article with three to eight setae. Claw large, undivided, numerous pores with sensilla coeloconica on dorsodistal surface of claw (Fig. 16J).

Male (Fig. 12C): Sternite of segment 15 with subtransverse (Fig. 12C) to moderately convex (Fig. 16F) posteromedial margin. Sternite of first genital segment small, divided, with transverse posterior margin, bearing about 20 moderate to long setae on each half with slight to moderate concentration near posterior margin. Gonopod of three articles and tapering, seta-like terminal process (Fig. 16K,L), with many short spine-like projections along its inner margin; articles of gonopod each typically bear 10–12 setae; many setae on gonopod and first genital sternite curved, at least distally.

Larval stadia: Stadium LII with 8 pairs of legs and two pairs of limb-buds; 14 antennal articles, all elongate; 3+3 teeth on dental margin of maxillipede coxosternum, outer tooth more distant than inner pair; tarsi unjointed. Stadium LIII with 10 pairs of legs and two pairs of limb-buds; 25 antennal articles; maxillipede dentition as in stadium LII; single tarsal articulation faintly defined on many legs.

Discussion. All specimens of *Henicops milledgei* share a large space between the outer and middle tooth of the maxillipede coxosternum (more than twice the distance between the inner and middle tooth), exceeded only by *H. brevilabiatus*. No notable geographic variation has been detected between populations of *H. milledgei* from different regions of *Nothofagus* forest in Victoria.

Segmentation of the larval antenna of *Henicops milledgei* and *H. tropicanus* presents a character that may be autapomorphic for *Henicops* or a group within the genus. Larval stadium LIII in both species has a uniquely high number of antennal articles (25), a count retained in larval stadium LIV in *H. tropicanus* at least. In comparison, *Lamyctes emarginatus* (=*fulvicornis*) and *L. coeculus* have only 14 articles in stadium LIII, and Lithobiidae have 14–17 articles in this stadium (Andersson, 1979: table III). Of Lithobiomorpha for which larval ontogeny has been described, only *Cermatobius longitarsis* approaches *Henicops* in having 20–24 articles in stadium LIII (Murakami, 1960; Andersson, 1979).

Synoptic classification of Henicopidae

Synoptic classifications of Henicopidae were most recently published by Attems (1914, 1928). These predate the description of many species, particularly by R.V. Chamberlin, and changes to generic classification. The following list encapsulates the current classification of henicopid species, together with distributional data.

Type species are indicated by an asterisk. Junior subjective synonyms are indicated following the senior synonym. Many of the named species of *Lamyctes* may, upon restudy, fall into synonymy, but published names that have not been synonymized in published work are listed as valid. Literature sources for synonymies are indicated.

Division of Henicopini into two clades (Edgecombe & Giribet, 2003b) is accommodated by a *Lamyctes-Henicops* Group and *Paralamyctes*.

Family Henicopidae Pocock, 1901b

(= Cermatobiidae by ICZN Opinion 1228)
Subfamily Henicopinae Pocock, 1901b
Tribe Henicopini Pocock, 1901b

Lamyctes-Henicops Group

Analamyctes Chamberlin, 1955
  **Analamyctes tucumanus* Chamberlin, 1955 (Argentina: Tucumán)
  Paralamyctes andinus Silvestri, 1903 (Argentina: Mendoza)
Easonobius Edgecombe, 2003a
  **Easonobius tridentatus* Edgecombe, 2003a (New Caledonia)
  Paralamyctes humilis Ribaut, 1923 (New Caledonia)
Henicops Newport, 1844
  **Henicops maculatus* Newport, 1844 (Australia: Tasmania, Victoria, New South Wales, Australian Capital Territory; New Zealand) (=*Henicops impressus* Hutton, 1877 *fide* Archey, 1937) (New Zealand)
  Lamyctes brevilabiatus Ribaut, 1923 (New Caledonia)
  Henicops dentatus Pocock, 1901a (=*Henicops oligotarsus* Attems, 1911; n.syn.) (Australia: Western Australia)
  Henicops milledgei n.sp. (Australia: Victoria)
  Henicops tropicanus n.sp. (Australia: Queensland)
Lamyctes Meinert, 1868 (=*Lamyctinus* Silvestri, 1909a; *Metalamyctes* Verhoeff, 1941)
Lamyctes (Lamyctes) Meinert, 1868
  **Lamyctes fulvicornis* Meinert, 1868 (junior subjective synonym of *Henicops emarginatus* Newport, 1844 *fide* Eason, 1996)
  Lamyctes adisi Zalesskaja, 1994 (Brazil: central Amazonas)
  Lamyctes albipes Pocock, 1894 (Java) (=?*L. mauriesi* Demange, 1981 *fide* Eason & Enghoff, 1992) (Guadeloupe, Canary Islands, Seychelles)
  Lamyctes anderis Chamberlin, 1955 (Peru; Bolivia)
  Lamyctes andinus Kraus, 1954 (Peru) (=*L. neglectus* Chamberlin, 1955; *L. rectus* Chamberlin, 1955; ?*L. subtropicalis* Chamberlin, 1955; synonymies *fide* Kraus, 1957) (Chile; Peru)
  Lamyctes caducens Chamberlin, 1938 (USA: New Mexico)
  Lamyctes cairensis Chamberlin, 1921 (Egypt)
  Lamyctes calbucensis Verhoeff, 1939 (Chile)
  Lamyctes cerronus Chamberlin, 1957 (Peru)
  Lithobius coeculus Brölemann, 1889 (Italy and other European greenhouse records; Canary Islands; Australia: New South Wales, Lord Howe Island; Argentina (Tucumán); Venezuela; Cuba; Mexico; USA: Hawaii, Illinois; Israel; Tanzania; Democratic Republic of Congo) (type species of *Lamyctinus* Silvestri, 1909a)
  Lamyctes cuzcotes Chamberlin, 1944 (Peru) (=*L. alancayanus* Chamberlin, 1955 *fide* Kraus, 1957)
  Lamyctes diffusus Chamberlin & Mulaik, 1940 (USA: Texas)
  Henicops emarginatus Newport, 1844 (=*Lamyctes chathamensis* Archey, 1917; *L. kermadecensis* Archey, 1917; ?*L. munianus* Chamberlin, 1920; ?*L. navaianus* Chamberlin, 1920; *L. neozelanicus* Archey, 1917; *L. tasmanianus* Chamberlin, 1920; *L. zelandicus* Chamberlin, 1920; synonymies *fide* Archey, 1937) (Chatham Islands; New Zealand; Fiji; Kermadec Islands; Tasmania) (=*L. fulvicornis* Meinert, 1868 *fide* Eason, 1996) (widespread in Europe and USA; Greenland; Iceland; Kurile Islands; eastern Africa: Ethiopia, Kenya, Somalia, Tanzania; Brazil: central Amazonas; Canary and Azore Islands; New Caledonia; Australia: Western Australia, South Australia, Victoria, New South Wales) (=*L. fulvicornis* var. *hawaiiensis* Silvestri, 1904 *fide* Zapparoli & Shelley, 2000) (Hawaii)
  Lamyctes gracilipes Takakuwa, 1940 (Ôagari, Ryukyu Islands)
  Lamyctes guamus Chamberlin, 1946 (Guam; Torijima Island)
  Lamyctes guamus koshiyamai Shinohara, 1957 (Japan)
  Lamyctes hellyeri Edgecombe & Giribet, 2003a (Australia: Tasmania, probably introduced)
  Henicops inermipes Silvestri, 1897 (Argentina: Salta)
  Lamyctes insulanus Verhoeff, 1941 (Fernando Po)
  Lamyctes leon Chamberlin, 1944 (Mexico)
  Lamyctes leleupi Matic & Darabantu, 1977 (Saint Helena)
  Lamyctes liani Larwood, 1946 (India)
  Lamyctes medius Chamberlin, 1951 (Angola; Democratic Republic of Congo; Gabon)
  Lamyctes neotropicus Turk, 1955 (Peru)
  Lamyctes nesiotes Chamberlin, 1952 (Bahamas)

Lamyctes omissus Kraus, 1957 (Peru)
Lamyctes orthodox Chamberlin, 1951 (Angola; Gabon)
Lamyctes oticus Archey, 1921 (New Zealand)
Lamyctes pachypes Takakuwa, 1941 (Japan; far eastern Russia)
Lamyctes pacificus Silvestri, 1905 (Chile) [subspecies of *L. inermipes* (Silvestri) *fide* Demange & Silva, 1976]
Lamyctes pinampus Chamberlin, 1910 (USA: Nevada, California)
Lamyctes pius Chamberlin, 1911a (USA: North Carolina, Georgia, New Jersey, Pennsylvania)
Lamyctes remotior Chamberlin, 1955 (Bolivia)
Lamyctes taulisensis Kraus, 1954 (Peru) (=*L. brattstroemi* Chamberlin, 1955 *fide* Kraus, 1957) (Chile)
Lamyctes tivius Chamberlin, 1911a (USA: Mississippi, Louisiana, Alabama)
Lamyctes tolucanus Chamberlin, 1943 (Mexico)
Lamyctes transversus Chamberlin, 1962 (Chile)
Lamyctes (Metalamyctes) Verhoeff, 1941
**Henicops africanus* Porat, 1871 (South Africa: widespread; Cameroon; Gabon; Democratic Republic of Congo; Madagascar; Juan Fernandez; Madagascar; Hawaii; Western Australia) (=*H. insignis* Pocock, 1891 *fide* Attems, 1928)
Lamyctes baeckstroemi Verhoeff, 1923 (erected as subspecies of *L. insignis* (Pocock)) (Juan Fernandez)
Lamyctes castaneus Attems, 1909 (South Africa: Western Cape, Eastern Cape, KwaZulu-Natal, Northern Province; Lesotho; Zimbabwe)
Lamyctes microporus Attems, 1909 (South Africa: Northern Cape)
Lamyctes neglectus Lawrence, 1955a (South Africa: KwaZulu-Natal); homonym of *L. neglectus* Chamberlin, 1955
Lamyctes robustus Lawrence, 1955b (South Africa: Eastern Cape; Lesotho; Namibia; Zimbabwe)
Henicops tristani Pocock, 1893 (Tristan d'Acunha; Madagascar)
Lamyctopristus Attems, 1928
Lamyctopristus (Lamyctopristus) Attems, 1928
**Lamyctopristus validus* Attems, 1928 (South Africa: Western Cape) (=*Lamyctopristus granulosus* Lawrence, 1955b) (South Africa: Western Cape)
Lamyctopristus (Eumyctes) Chamberlin, 1951 (=*Neomyctes* Chamberlin, 1951)
**Henicops sinuatus* Porat, 1893 (South Africa: Western Cape, Northern Cape)
Lamyctes denticulatus Attems, 1907 (South Africa: Western Cape; Democratic Republic of Congo)
Lamyctes ergus Chamberlin, 1951 (type of *Neomyctes* Chamberlin, 1951) (Angola)
Lamyctes numidicus Latzel, 1886 (Algeria; Gabon)
?*Lamyctes setigerus* Lawrence, 1955b (South Africa: KwaZulu-Natal, Northern Province; Zambia)
Pleotarsobius Attems, 1909
**Lamyctes heterotarsus* Silvestri, 1904 (Hawaii)

Paralamyctes Group

Paralamyctes Pocock, 1901b (=*Haasiella* Pocock, 1901b; *Triporobius* Silvestri, 1917)
Paralamyctes (Paralamyctes) Pocock, 1901b (=*Triporobius* Silvestri, 1917)
**Paralamyctes spenceri* Pocock, 1901b (South Africa: Western Cape, KwaZulu-Natal, Northern Province; Swaziland; Madagascar)
Paralamyctes asperulus Silvestri, 1903 (South Africa: Western Cape, Eastern Cape) (=*P. tabulinus* Attems, 1928 *fide* Edgecombe, 2003b)
Lamyctes bipartitus Lawrence, 1960 (Madagascar)
Paralamyctes harrisi Archey, 1922 (New Zealand)
Paralamyctes levigatus Attems, 1928 (South Africa: Western Cape)
Paralamyctes (Paralamyctes) monteithi Edgecombe, 2001 (Australia: Queensland)
Paralamyctes (Paralamyctes) neverneverensis Edgecombe, 2001 (Australia: New South Wales)
Triporobius newtoni Silvestri, 1917 (India)
Paralamyctes (Paralamyctes) prendinii Edgecombe, 2003b (South Africa: Western Cape)
Paralamyctes quadridens Lawrence, 1960 (Madagascar)
Paralamyctes tridens Lawrence, 1960 (Madagascar)
Paralamyctes weberi Silvestri, 1903 (South Africa: Western Cape)
Paralamyctes (Haasiella) Pocock, 1901b (=*Wailamyctes* Archey, 1917)
**Henicops insularis* Haase, 1887 (New Zealand: Auckland Islands) (=*Wailamyctes munroi* Archey, 1923 *fide* Johns, 1964) (New Zealand: Auckland Islands)
Paralamyctes (Haasiella) cammooensis Edgecombe, 2004a (Australia: Queensland, New South Wales)
Paralamyctes (Haasiella) ginini Edgecombe, 2004a (Australia: New South Wales, Australian Capital Territory)
Wailamyctes halli Archey, 1917 (New Zealand)
Paralamyctes (Haasiella) subicolus Edgecombe, 2004a (Australia: Tasmania)

Wailamyctes trailli Archey, 1917 (New Zealand)
Paralamyctes (Nothofagobius) Edgecombe, 2001
**Paralamyctes (Nothofagobius) cassisi* Edgecombe, 2001 (Australia: New South Wales)
Paralamyctes (Nothofagobius) mesibovi Edgecombe, 2001 (Australia: Tasmania)
Paralamyctes (Thingathinga) Edgecombe, 2001
**Paralamyctes (Thingathinga) grayi* Edgecombe, 2001 (Australia: New South Wales)
Paralamyctes (Thingathinga) hornerae Edgecombe, 2001 (Australia: New South Wales)
Paralamyctes validus Archey, 1917 (=*P. dubius* Archey, 1917 *fide* Archey, 1921, 1937) (New Zealand)
Paralamyctes subgen. undet.
Henicops chilensis Gervais in Walckenaer & Gervais, 1847 (Chile; Argentina: Neuquén, Rio Negro)
Paralamyctes wellingtonensis Edgecombe, 2003c (Chile)

Tribe Zygethobiini Attems, 1914

Buethobius Chamberlin, 1911a
**Buethobius oabitus* Chamberlin, 1911a (USA: Mississippi)
Buethobius arizonicus Chamberlin, 1945a (USA: Arizona)
Buethobius conjugans Chamberlin, 1911b (USA: California)
Buethobius heustoni Williams & Hefner, 1928 (USA: Ohio)
Buethobius translucens Williams & Hefner, 1928 (USA: Ohio)
Cermatobius Haase, 1885 (=*Esastigmatobius* Silvestri, 1909a *fide* Würmli, 1977)
**Cermatobius martensii* Haase, 1885 (Indonesia: Adenara)
Esastigmatobius japonicus Silvestri, 1909a (Japan) (type species of *Esastigmatobius* Silvestri, 1909a)
Esastigmatobius curticornis Chamberlin & Wang, 1952 (Japan)
Esastigmatobius kirgisicus Zalesskaja, 1972 (Kirghizia)
Esastigmatobius longicornis Takakuwa, 1939 (Japan; Taiwan)
Esastigmatobius longitarsis Verhoeff, 1934b (Japan; Taiwan)
Hedinobius Verhoeff, 1934a
**Hedinobius hummelii* Verhoeff, 1934a (western China)
Yobius Chamberlin, 1945b
**Yobius haywardi* Chamberlin, 1945b (USA: Utah)
Zygethobius Chamberlin, 1903 (=*Zantethobius* Chamberlin, 1911a)
**Henicops dolichopus* Chamberlin, 1902 (USA: Utah, California)
Zygethobius columbiensis Chamberlin, 1912 (Canada: British Columbia)
Zygethobius ecologus Chamberlin, 1938 (USA: Oregon)
Zygethobius (Zantethobius) pontis Chamberlin, 1911a (USA: Virginia, Tennessee) (type of *Zantethobius* Chamberlin, 1911a)
Zygethobius sokariensis Chamberlin, 1911b (USA: California)

Henicopinae of uncertain affinity

Remylamyctes Attems, 1951
**Remylamyctes straminae* Attems, 1951 (Madagascar)

Subfamily Anopsobiinae Verhoeff, 1907

Anopsobius Silvestri, 1899 (=*Promethon* Chamberlin, 1962; =*Tasmanobius* Chamberlin, 1920)
**Anopsobius productus* Silvestri, 1899 (Chile)
Anopsobius actius Chamberlin, 1962 (Chile)
Anopsobius (Promethon) diversus Chamberlin, 1962 (Chile)
Dichelobius giribeti Edgecombe, 2004b (Australia: New South Wales, Australian Capital Territory, Victoria, Lord Howe Island)
Anopsobius macfaydeni Eason, 1993 (Falkland Islands)
Anopsobius neozelanicus Silvestri, 1909a (New Zealand)
Anopsobius patagonicus Silvestri, 1909a (Argentina: Santa Cruz)
Anopsobius patagonicus calcaratus Attems, 1928 (South Africa: Western Cape; possibly introduced *fide* Lawrence, 1984)
Tasmanobius relictus Chamberlin, 1920 (Australia: Tasmania)
Dichelobius schwabei Verhoeff, 1939 (Chile)
Anopsobius wrighti Edgecombe, 2003d (Australia: New South Wales)
Anopsobiella Attems, 1938
**Anopsobius (Anopsobiella) dawydoffi* Attems, 1938 (Vietnam)
Catanopsobius Silvestri, 1909b
**Catanopsobius chilensis* Silvestri, 1909b (Chile)

Dichelobius Attems, 1911
 **Dichelobius flavens* Attems, 1911 (Australia: Western Australia)
 Dichelobius bicuspis Ribaut, 1923 (New Caledonia)
Ghilaroviella Zalesskaja, 1975
 **Ghilaroviella valiachmedovi* Zalesskaja, 1975 (Tajikistan)
Rhodobius Silvestri, 1933
 **Rhodobius lagoi* Silvestri, 1933 (Rhodes)
Shikokuobius Shinohara, 1982
 **Anopsobius japonicus* Murakami, 1967 (Japan)

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Beach Flies (Diptera: Tethinidae: Tethininae) From Australia and Papua New Guinea, with Descriptions of Two New Genera and Ten New Species

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ABSTRACT. This paper deals with the subfamily Tethininae of the Beach Flies Tethinidae from Australia and Papua New Guinea. Two new genera and ten new species are described: *Sigaloethina phaia* n.gen. and n.sp., *Thitena cadaverina* n.gen. and n.sp., *Dasyrhicnoessa atripes* n.sp., *D. ciliata* n.sp, *D. humilis* n.sp., *D. longisetosa* n.sp., *D. macalpinei* n.sp., *D. ostentatrix* n.sp., *D. pallida* n.sp., and *D. priapus* n.sp. A new species group, the *Dasyrhicnoessa ciliata*-group, is proposed. It differs from congeners primarily in its long-haired arista, slender body and legs, and peculiarities in the male terminalia. New records for Australia and Papua New Guinea are also given for species previously described. The recently described *Dasyrhicnoessa clandestina* Munari, 2002 is recorded for the second time from Fiji where it was found in association with *D. insularis* (Aldrich, 1931). A key is proposed to all genera and species of Tethininae known from Australia and Papua New Guinea. An updated checklist to the world species of *Dasyrhicnoessa* as well as a catalogue of the Tethininae of Australia and Papua New Guinea are also given.

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Tethinids are small flies chiefly inhabiting the temperate and tropical shores of all seas and oceans of the world. Some species are also found inland, associated with saline environments, in particular continental salt lakes and alkaline hot springs. Within the family, many species seem to be strictly dependent on proximity to the sea, i.e. true thalassophilous flies mostly inhabiting the intertidal zone, wrack heaps, salt marshes, dune vegetation, lagoon-litoriparian zones, mangroves (particularly species of *Dasyrhicnoessa* Hendel), and salty soils or bare sand. Other species are more widely halophilous, and are commonly found on various types of saline biotopes, irrespective of the presence of littoral environments. Some species in the subfamily Pelomyiinae are associated with meadows that occur in mountain passes, forests, and desert oases. In the subfamily Apetaeninae, a few subantarctic species occur on seabird guano and are strictly associated with colonies of penguins and other shorebirds. Tethinids are also recorded from habitats that have been adversely modified by human activity, such as meadows polluted by industrial emissions (Bährmann, 1982) or slaughterhouses and poultry farms (Zuska & Laštovka, 1969). These synanthropic habitats are usually sites of salt accumulation and enrichment. The biology and immature stages of this family are poorly known (for a brief synopsis see Mathis & Munari, 1996). Often sites where tethinids occur have numerous individuals of only a few species.

The family is subdivided into five subfamilies that include 15 genera with approximately 160 species (including the new taxa described in the present work).

Historical review

Records of beach flies from Australia and Papua New Guinea are fragmentary. The oldest citation of tethinids from Australia dates to 1924, when Malloch described *Tethina nigriseta* from Woolgoolga, NSW. This is a very common species on the eastern seashores of Australia. Later, Malloch (1935) described *Tethina (Macrotethina) tibiseta* (a junior synonym of *Pseudorhicnoessa spinipes*), *Dasyrhicnoessa fulvescens* and *D. serratula* from Townsville, Qld. In the same paper, Malloch also described *Tethina (Tethina) pallidiseta* from Collaroy, NSW, a common species in southern and eastern Australia, and he listed *T. nigriseta* from Sydney and Townsville.

The subfamily Zaleinae has an uncertain systematic position between Canacidae and Tethinidae (themselves in turn possible subgroups of a same family) and comprising species with transitional features that prevent satisfactory and reliable taxonomic attribution. D.K. McAlpine (1982, 1985) designated the new subfamily and described the genus *Zalea* represented by three species from New Zealand and New South Wales. A few years later, Colless & D.K. McAlpine (1991) published an important synopsis dealing with the Australian flies, in which the family Tethinidae was concisely defined and included illustrations (head and wing) of *Tethina nigriseta*.

In the only work specifically dealing with beach flies from southwestern Australia, Munari (2000) described the genus *Plesiotethina*, with the single species *P. australis*, and the peculiar species *Tethina hirsuta*. Also, in the same paper, *Tethina ochracea* (Hendel) and *T. pallidiseta* Malloch were reported from southwestern Australia.

Most of the above-mentioned species are also recorded in Mathis & Sasakawa's (1989) and Mathis & Munari's (1996) catalogues dealing with Australasian/Oceanian and World faunas respectively. The citations reported in the two catalogues obviously take into account only the well known records from the literature and do not contain original distribution data. No Tethinid species have been previously recorded from Papua New Guinea.

Materials and methods

The present work is based on the study of more than 1400 specimens of Tethininae from the collection of the Australian Museum, Sydney. The material is mostly from the eastern coast of Australia with some specimens from elsewhere in Australia, Papua New Guinea and a few Pacific islands (for the latter localities see the final appendix). Most specimens are glued to triangular points or double mounted by minuten in blocks. Because specimens are small, usually less than 4 mm in length, study and illustration of male terminalia required use of dissecting and compound microscopes. In the text, genera and species as well as the localities of capture under each species, are listed in alphabetical order. Holotype and paratype label data are quoted without interpretation; a slash (/) indicates the end of a line of print or handwriting, two slashes (//) signifies another label. Significant supplementary or qualifying information is presented in brackets. The descriptions of new species are based primarily on their respective holotypes with variation being accounted for in the remarks section or directly added in the description itself.

Under the description of each new species, the holotype measurements are given with paratype range between parentheses where appropriate. The morphological terminology chiefly follows that published in the Manual of Nearctic Diptera (J.F. McAlpine, 1981), except for the first antennal flagellomere for which the term "postpedicel" (*sensu* Stuckenberg, 1999) has been used. The fine figures illustrating the habitus of both *Sigaloethina phaia* and *Thitena cadaverina*, as well as the scutellum of the latter species, have been skillfully drawn and inked by Mrs. Gioiella D'este (courtesy of MCV), an artist of the Natural History Museum, Venice. All remaining figures, mostly illustrating male terminalia, were drawn and inked by the author.

Acronyms for museums, especially to indicate the deposition of a primary type: AM, Australian Museum, Sydney, Australia; BMNH, The Natural History Museum [former British Museum (Natural History)], London, England; BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA; DEI, Deutsches Entomologisches Institut, Eberswald, Germany; MCV, Natural History Museum, Venice, Italy; NMW, Naturhistorisches Museum, Vienna, Austria; TAU, Tel Aviv University, Tel Aviv, Israel; USNM, National Museum of Natural History (former United States National Museum), Smithsonian Institution, Washington, D.C., USA; ZSM, Zoologische Staatssammlung München, Germany. Abbreviations for primary types: HT, holotype; and LT, lectotype. States and territories of Australia are abbreviated as follows: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; TAS, Tasmania; VIC, Victoria; WA, Western Australia.

Key to genera and species of Tethininae from Australia and Papua New Guinea

Note: the following key should be regarded as preliminary, particularly with regard to the species of the genus *Dasyrhicnoessa*, due to the marked similarity among species as well as the scarcity of available material. The characters of the male specimens are used because female features are not diagnostic. *Plesiotethina australis* has been provisionally inserted in the key for practical purposes, although it may not belong in the Tethininae as it "may be regarded as a possible sister group either to *Tethina* or even to the entire subfamily Tethininae" (Munari, 2000). Conversely, *Dasyrhicnoessa serratula* has been intentionally excluded from the key because of its doubtful specific status (see text).

1 Disc of scutellum setulose (Fig. 30); at least mid and hind tibiae with strong setae 2

—— Disc of scutellum bare; tibiae usually evenly setulose, bearing short setae and setulae (except for *Tethina hirsuta* having legs strongly setulose) 3

2 Costal vein abbreviated, not extending beyond end of vein R_{4+5}; legs of male normally setulose, without long villosity; at least hind femur and tibia with more or less extended apical dark ring; 6 rows of acrostichal setulae on anterior half of scutum ...... *Pseudorhicnoessa spinipes* Malloch

—— Costal vein not abbreviated, reaching end of M_1; legs of male, in particular forelegs, bearing characteristic long and thick villosity (Fig. 29); femora and tibiae unicolorous; 8–9 rows of acrostichal setulae on anterior half of scutum .... *Thitena cadaverina* n.gen. and n.sp.

3 Lower face, just above vibrissal angle, with small, shining, sclerotized tubercle; anterior surstylus of male terminalia absent [genus *Tethina* Haliday] 4

—— Lower face simple, without shining, sclerotized tubercle; anterior surstylus of male terminalia present 7

4 Setal vestiture of body and legs whitish .... *Tethina pallidiseta* Malloch

—— Setal vestiture of body and legs black 5

5 Legs with tibiae bearing rows of strong, posterodorsal setae; 5 (2+3) dorsocentral setae; abdomen distinctly setose, in any case always with setae much more numerous, stronger, and longer than congeners .... *Tethina hirsuta* Munari

—— Legs with tibiae evenly setulose, bearing short black setae and setulae; 4 (1+3) dorsocentral setae; abdomen with unmodified setation 6

6 Lateral profile of head with vertically flattened face; longitudinal, subshining stripe of gena distinctly broad; acrostichal setulae usually in 2–3 rows; terminalia of male with surstylus bearing numerous, stout spinulae about as long as or shorter than thickness of apical part of surstylus in posterior view .... *Tethina ochracea* (Hendel)

—— Lateral profile of head with face not vertically flattened but slightly depressed; gena uniformly microtomentose, without longitudinal, subshining stripe; 4 rows of acrostichal setulae; terminalia of male with surstylus bearing numerous, very long, stout spinulae, mostly distinctly longer than thickness of apical part of surstylus in posterior view (Fig. 28) .... *Tethina nigriseta* Malloch

7 Body cuticle distinctly glossy dark brown; anterior surstylus of male terminalia distinctly larger than posterior surstylus, arising from extremity of lower apical part of epandrium, and bearing characteristic triangular patch of microtrichia on outer surface (Fig. 24) .... *Sigaloethina phaia* n.gen. and n.sp.

—— Body cuticle distinctly dull to translucent yellowish, generally covered with more or less dense microtomentum; anterior surstylus of male terminalia usually smaller than posterior surstylus, never arising from extremity of lower apical part of epandrium, and without patch of microtrichia on outer surface 8

8 Eye without interfacetal setulae; vibrissal angle of gena poorly marked, gently curved upwards; true vibrissa absent; acrostichal setulae short and thin, almost microscopic in male; ctenidium of fore femur absent; anterior surstylus of male terminalia rudimentary, reduced to small, knoblike sclerite bearing cluster of long, thin setulae .... *Plesiotethina australis* Munari

—— Eye densely micropubescent; vibrissal angle of gena strongly marked; true vibrissa present; acrostichal setulae of normal length in both sexes; ctenidium of fore femur variable; anterior surstylus of male terminalia more or less developed, never rudimentary or knoblike [genus *Dasyrhicnoessa* Hendel] 9

9 Abdomen with 3 (2 lateral and 1 median) dark, rounded spots on each tergite .... *Dasyrhicnoessa tripunctata* Sasakawa

—— Abdomen without dark, rounded spots 10

10 Arista bearing distinctly long, spaced hairs (Fig. 8); body and legs bright yellow to yellowish; slender flies [*ciliata*-group] 11

—— Arista micropubescent to short-haired (Fig. 7); colour of body and legs variable; flies of usual aspect within genus 13

11 Fore femur with ctenidial comb formed by short, strong, black spinulae, in females distinctly weaker and thinner; 4 rows of acrostichal setulae; mid femur of male with posteroventral armature formed by spine-like, black setae arranged on entire length of femur; posterior surstylus of male terminalia lacking characteristic cluster of thin setulae on inner side (Figs. 5–6) .... *Dasyrhicnoessa ciliata* n.sp.

—— Fore femur lacking true ctenidium, only weak row of thin setulae present; 5–6 rows of acrostichal setulae; mid femur of male with posteroventral armature formed by spine-like, black setae mostly arranged on distal half of femur; posterior surstylus of male terminalia with characteristic cluster of thin setulae on inner side (Figs. 11–12, 20–21) 12

12 Setae of mesonotum long, distinctly longer than ones of congeners; postocular setae of normal size; last tarsomere of legs very slightly infuscated; cerci of male terminalia small, in lateral view as long as anterior surstylus (Figs. 11–12) .... *Dasyrhicnoessa longisetosa* n.sp.

—— Setae of mesonotum of normal size; postocular setae somewhat long and very distinctive; tarsi homogeneously yellowish; cerci of male terminalia strikingly longer and broader than ones of congeners, in lateral view noticeably longer than anterior surstylus (Figs. 20–21) .... *Dasyrhicnoessa priapus* n.sp.

13 Hind tibia of male bearing long, thin, yellowish pubescence on posteroventral distal half; male terminalia (Figs. 13–14) with epandrium bearing characteristic cluster of 8–9 very long setae on entire anteroventral part; anterior surstylus strongly reduced, hardly visible in lateral view; cerci long and narrow in both lateral and caudal views; small-sized, body length < 1.4 mm .... *Dasyrhicnoessa macalpinei* n.sp.

—— Hind tibia evenly setulose, bearing short setae and setulae; male terminalia with epandrium not as above, at most bearing 3 long setae on anteroventral part (Fig. 9), in latter case cerci distinctly stumpy; anterior surstylus more or less developed, always well discernible in lateral view; cerci not as above; body length > 1.4 mm 14

14 Mid and hind legs with last tarsomere pitch-black, and foreleg with distal two tarsomeres of same colour, strongly contrasting with remaining yellowish tarsomeres; terminalia of male horseshoe-shaped in posterior view (Fig. 4) .... *Dasyrhicnoessa atripes* n.sp.

—— Distal tarsomeres of legs at most slightly infuscated; terminalia of male not as above 15

15 Acrostichal setulae in 4 rows irregularly arranged on anterior half of scutum; yellow species with first three tergites of abdomen widely pitch-black (this character must be verified by examination of more abundant material), strongly contrasting with remaining tergites; setal vestiture of mesonotum pale brownish to golden yellow; fore femur lacking true ctenidium .... *Dasyrhicnoessa fulvescens* Malloch

—— Acrostichal setulae in 6 distinct rows on anterior half of scutum; darker species having brownish yellow to dark grey thorax; first three tergites of abdomen differently coloured, never strongly contrasting with remaining tergites; setal vestiture of mesonotum distinctly brown to black, often with setae showing golden reflections; presence of true ctenidium variable 16

16 Gena with distinct, longitudinal, apparently translucent, narrow stripe; abdomen with posterior surstyli of male terminalia noticeably and characteristically exposed outwardly .... *Dasyrhicnoessa ostentatrix* n.sp.

—— Gena homogeneously microtomentose; abdomen with posterior surstyli of male terminalia partially to fully hidden inside postabdominal sclerites 17

17 Posteroventral armature of male mid femur with distal part characteristically crest-shaped, formed by strong, close, black spinulae abruptly decreasing in length distally; anterior surstylus of male terminalia large, paddle-shaped, very much longer than small knoblike posterior surstylus .... *Dasyrhicnoessa ferruginea* (Lamb)

—— Posteroventral armature of male mid femur with distal part not crest-shaped, at most entire armature formed by regularly spaced spinulae gradually decreasing in length on distal third; anterior surstylus of male terminalia distinctly to slightly shorter than posterior surstylus, latter never knoblike 18

18 Anterior surstylus of male terminalia small, rodlike or similar to short lobe, bearing few apical hairs (Figs. 9, 18) 19

—— Anterior surstylus of male terminalia noticeably broad, not rodlike or short lobe-shaped, bearing numerous microspinulae or strong setae on posterior and apical margins 21

19 True ctenidium of fore femur present; posterior surstylus of male terminalia posteriorly directed (lateral view), bearing characteristic row of long, strong setae on lower edge (anterior margin) .. *Dasyrhicnoessa sexseriata* (Hendel)

—— True ctenidium of fore femur absent; posterior surstylus of male terminalia vertically directed (lateral view), bearing more or less sparse, microscopic hairs on anterior margin (Figs. 9, 18) 20

20 Golden yellow patches on both sides of ocellar triangle somewhat broad, merging before anterior ocellus; longest diameter of eye about 5.6× genal height; anterior surstylus of male terminalia short and squat, lobe-shaped; posterior surstylus (lateral view) stumpy, subquadrate, medially only slightly wider than long, pointed apically (Fig. 9) .... *Dasyrhicnoessa humilis* n.sp.

—— Golden yellow patches on both sides of ocellar triangle separated, generally not merging before anterior ocellus; longest diameter of eye about 4.5× genal height; anterior surstylus of male terminalia relatively long and thin; posterior surstylus (lateral view) moderately slender, lobe-shaped, distinctly longer than wide, rounded apically (Fig. 18) .... *Dasyrhicnoessa pallida* n.sp.

21 Yellowish species; anterior surstylus of male terminalia large, subquadrate to subtrapezoidal (lateral view), having both posterior and ventral margins microscopically and very irregularly serrated, bearing some sparse, marginal microspinulae .... *Dasyrhicnoessa vockerothi* Hardy & Delfinado

—— Noticeably darker species, brownish grey to dark grey; anterior surstylus of male terminalia distinctly subrectangular in lateral view, kidney-shaped in posterior view, bearing several, close, long and strong setae on both posterior and apical margins .... *Dasyrhicnoessa insularis* (Aldrich)

Taxonomic account

Dasyrhicnoessa atripes n.sp.

Figs. 1–4

Type material. HOLOTYPE ♂, **Australia, New South Wales** "NSW: Wategos / Beach, Cape Byron / 7 Nov. 2000 // Beach, Cape Byron / 7 Nov. 2000 [*sic*] // HOLOTYPUS / *Dasyrhicnoessa* / *atripes* sp. n. ♂ / L. Munari des." AM K186735. The specimen is headless (see text), for the rest it is in excellent condition, and is double mounted (glued on the tip of a triangular card); abdomen dissected, stored in glycerol in a small plastic tube, and pinned below the specimen.

Description. *Size*. Body length about 2.3 mm (supposed), wing length 1.92 mm, wing width 0.75 mm. *Habitus*. Grey species with yellow legs and yellowish grey wings. All setae and setulae black, except for abdominal setae having golden reflections. *Head*. Missing. Nevertheless, considering that the morphological characters as well as the chaetotactic pattern of the head in most species belonging to this genus are not very informative at the specific level, I have judged it reasonable to name and describe the new species since the rest of the specimen is in excellent condition. *Thorax*. Entirely dark brown, covered with grey microtomentum; 1+3 dorsocentral setae; 6 rows of acrostichal setulae on anterior half of scutum, otherwise arranged in 4–6 rows; prescutellar acrostichals long and strong; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta long and strong, anterior setae shorter and distinctly weaker; 1 long presutural seta; 2 notopleurals about subequal in length; 1 supra-alar, below it 1 shorter and weaker seta; 2 postalars, external one distinctly longer and stronger; scutellum with apical area yellowish, bearing 4 long marginal setae, apical ones longer; both proepisternal and proepimeral setae present; anepisternum with several long setulae, and 3 long, posteriorly directed, postero-marginal setae, mid one longer and stronger, and 1 erect seta at posterodorsal margin; katepisternum with scattered, short pubescence, bearing long and strong posterodorsal seta; anepimeron, katatergite and meron without setae and setulae. *Legs*. Entirely yellow, except for last tarsomeres which are pitch-black; evenly setulose, bearing short black setae and setulae; foreleg having coxa with long and strong setae, and femur with long posterodorsal and posteroventral setae, latter ones on apical half only; fore femur with ctenidial comb formed by short, black spinulae antero-ventrally on distal third; mid femur with comb of posteroventral, short, spine-like setae, decreasing in length distally; hind femur not swollen; mid and hind legs with last tarsomere pitch-black, foreleg with last two tarsomeres of same colour, strongly contrasting with remaining yellowish tarsomeres. *Wing*. Veins yellowish, membrane yellowish grey; alula with fringe formed by several, close, long, black setae; costal vein reaching end of M_1, bearing several, short, spaced, microscopic setulae on dorsal and ventral surfaces; R_{2+3} slightly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending at basal third of cell *dm*; crossvein *dm-cu* distinctly shorter than half of last section of CuA_1; halter pale yellow. *Abdomen*. Blackish, with setal vestiture formed by dark setulae and black posteromarginal setae on each tergite, latter setae having golden reflections; transverse stripes at posterior edge of tergites somewhat broad, yellowish. *Male terminalia* (Figs. 1–4). Epandrium bearing pair of moderately long setae dorsally, and several short setae on remaining posterior surface; cercus small, pubescent, covered with microscopic hairs and with long setae dorsally; anterior surstylus stumpy in lateral view, narrow in posterior one, bearing sparse, thin setae on inner side; posterior surstylus very stumpy, bearing several spine-like setae on inner side; aedeagal apodeme long, straight, only slightly bent distally; ejaculatory apodeme large, as long as or slightly longer than half of aedeagal apodeme, with broad distal fan; distiphallus long, ribbon-like, micropubescent.

Female. Unknown.

Distribution. Australia (NSW).

Remarks. Additional material of this interesting species is needed to corroborate the consistency of the character state "colour of last tarsomeres pitch-black" and to see the head.

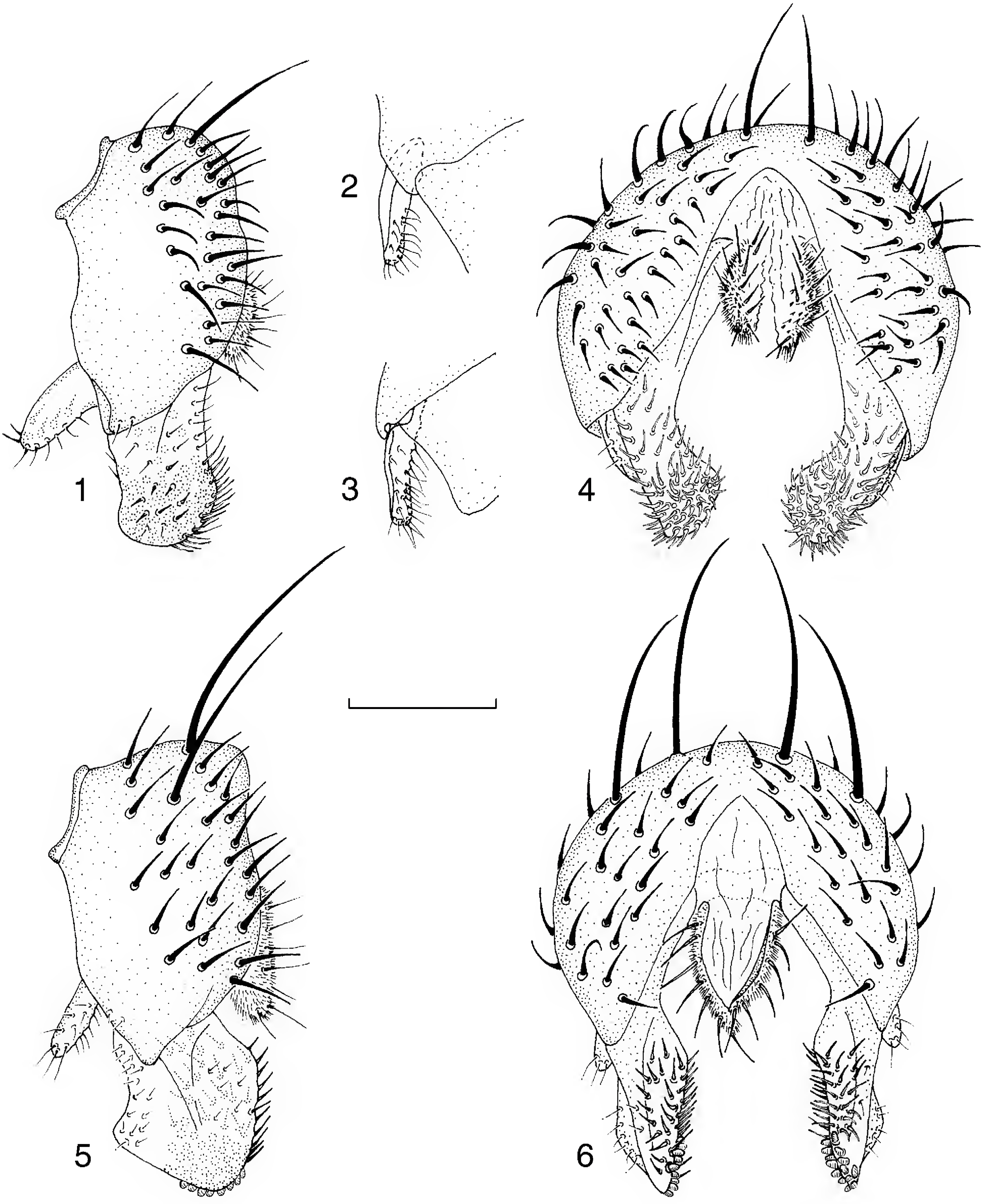
Etymology. Compound word, from the Latin *ater* meaning black and *pes* meaning foot. The specific epithet refers to the pitch-black last tarsomeres of the legs.

Dasyrhicnoessa ciliata n.sp.

Figs. 5–6

Type material. HOLOTYPE ♂, **Australia, Northern Territory** "NT: Buffalo Ck, / Darwin; 2–5 Mar. / 1996; D.K. McAlpine, / G.R. Brown" // "HOLOTYPUS / *Dasyrhicnoessa* / *ciliata* sp.n. ♂ / L. Munari des", AM K186736. The specimen is in excellent condition, and is double mounted (glued on the tip of a triangular card label); abdomen dissected, stored in glycerol in a small plastic tube, and pinned below the specimen. PARATYPES 2♀♀ same data as holotype. One paratype has an additional, orange label with handwritten "Laboulb." The holotype and one paratype are deposited in AM, the second paratype is preserved in MCV.

Description. *Size*. Body length 2.3 mm (2.1–2.3), wing length 1.9 mm (1.8–1.9), wing width 0.7 mm (0.67–0.72). *Habitus*. Yellow species with setal vestiture of thorax black. Head yellow with antenna bearing very long-haired arista. Wings yellowish grey. *Head*. Entirely yellow; frons, including orbital vittae, homogeneously yellow, except for usual golden yellow patch on both sides of ocellar triangle; paravertical setae well developed, inclinate; inner vertical seta slightly inclinate, strong, about as long as lateroclinate outer vertical seta; postocular and postgenal setae somewhat long, former setae in 1–2 rows; upper postocular seta long, inclinate towards inner vertical seta; ocellar triangle bearing pair of long, thin pseudopostocellar setae in addition to pair of strong ocellars; 2–3 very short, thin setulae between ocellars and pseudopostocellars; 3 strong, lateroclinate orbital setae; row of long, thin, inclinate setulae on orbital vitta between two anterior orbitals and frontals; 3 pairs of frontal setae, anterior one short and thin in male holotype, plus 2 pairs of thin setulae, all setae and setulae inclinate, mid pair with setae distinctly cruciate at apex; antenna with large and pubescent postpedicel, bearing blackish, very long-haired arista (Fig. 8); eye micropubescent, very large, distinctly oblong vertically, its longest diameter 5× as long



Figs. 1–6. Terminalia of male. *Dasyrhicnoessa atripes* n.sp.: (1) lateral view; (2) anterior surstylus posterolateral view; (3) anterior surstylus posterior view; (4) posterior view. *Dasyrhicnoessa ciliata* n.sp.: (5) lateral view; (6) posterior view. Scale bar: 0.1 mm.

as genal height; 6–8 blackish peristomal setae, three anteriors, including vibrissa, very strong and long; mouth parts pale yellow, with labellum shorter than length of buccal cavity, and palpus long, slightly clavate, bearing scattered setulae. *Thorax*. Entirely yellow, slightly translucent, with setal vestiture black; 1+3 long dorsocentral setae; 4 rows of acrostichal setulae on anterior half of scutum, otherwise arranged in 2–3 rows; posterior surface of scutum mostly bare (holotype); prescutellar acrostichals very long and strong; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta long and strong, anterior setae shorter and weaker; 1 long presutural seta; 2 notopleurals about subequal in length; 1 supra-alar, below it 1 shorter and weaker seta; 2 postalars, external one distinctly longer and stronger; scutellum with 4 long marginal setae; both proepisternal and proepimeral setae present; anepisternum with scattered pubescence, bearing 3 long, posteriorly directed, posteromarginal setae, middle one longer and stronger, and 1 erect, thin seta at posterodorsal margin; katepisternum with few scattered setulae and bearing long posterodorsal seta; anepimeron, katatergite and meron without setae and setulae. *Legs*. Evenly setulose, bearing short blackish to yellowish setae and setulae, except for foreleg having coxa with long, black setae, and femur with a few posterodorsal setae and remarkable row of very long, slightly curved, posteroventral setae; fore femur with ctenidium formed by long, strong, black spinulae (in female distinctly weaker); mid femur of male with row of long, spaced, spine-like, posteroventral black setae evenly arranged on entire length of femur; all legs, including coxae, yellow; last tarsomere slightly infuscate. *Wing*. Veins brownish yellow, membrane yellowish grey; alula with fringe formed by erect, black setae; costal vein reaching end of M_1, bearing several, spaced, microscopic setulae on dorsal and ventral surfaces; R_{2+3} slightly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending before middle of cell *dm*; crossvein *dm-cu* distinctly shorter than one third of last section of CuA_1; halter yellowish. *Abdomen*. Brown, bearing several thin setae and setulae; transverse stripes at posterior edge of tergites narrow, whitish. *Male terminalia* (Figs. 5–6). Epandrium bearing two pairs of very long setae dorsally, and several short setae on remaining posterior surface; cercus moderately long, pubescent, covered with microscopic hairs and with long setae dorsally; anterior surstylus small, simple, with sparse, thin setae on both outer and inner sides; posterior surstylus rather broad, with anterior outline markedly sinuous, lobe-shaped; inner side of posterior surstylus with many setae and apical cluster of short, stout tubercles; aedeagal apodeme long and straight; distal fan of ejaculatory apodeme poorly developed; distiphallus long, ribbon-like, bearing long micropubescence.

Female. Similar to male, except for slight sexual dimorphism. Abdomen pale reddish yellow, marked by medial, longitudinal, brown stripe, and with transverse stripes at posterior edge of tergites hardly discernible; apex of postabdomen with segments telescopically retractile. *Female terminalia*. Cerci moderately long, straight, setulose; spermathecae spherical, smooth.

Distribution. Australia (NT).

Remarks. This new species is characterized by a long-haired arista (an apomorphic character state with respect to the ground plan of the Tethinidae, Figs. 7–8) as well as by the very enlarged posterior surstylus of the male terminalia (Fig. 5). Both these peculiar features, in addition to the yellow body and legs, and the characteristic slender habitus of the flies, are also found in *D. longisetosa* and *D. priapus* (see below). In my opinion, these three species form a taxonomic group, named here "the *Dasyrhicnoessa ciliata*-group", in which *D. ciliata* would seem to be the sister species of the monophyletic clade *D. longisetosa* plus *D. priapus*, the latter two species additionally sharing a peculiar cluster of thin setulae arising from the medial side of posteromarginal surface of the posterior surstylus (Figs. 11–12, 20–21) as well as sharing the lack of a true ctenidium which is well developed in *D. ciliata*.

Etymology. From the Latin *ciliatum* meaning bearing eyelashes. The specific epithet refers to the long-haired arista of the antennal postpedicel.

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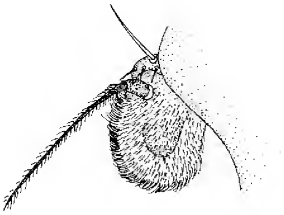

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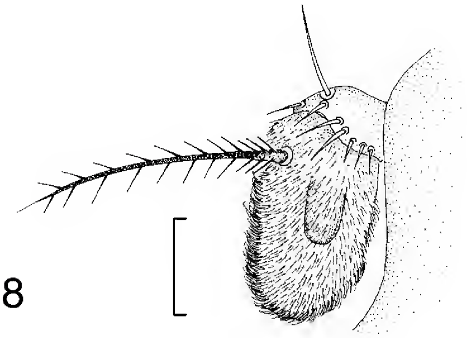


Figs. 7–8. Antenna: (7) *Dasyrhicnoessa* spp., aristal pubescence longest length; (8) *Dasyrhicnoessa ciliata* n.sp. Scale bar: 0.1 mm.

Dasyrhicnoessa ferruginea (Lamb, 1914)

Mathis & Sasakawa, 1989: 667; Mathis & Munari, 1996: 12; Munari & Evenhuis, 2000: 147.

Material examined. **Australia, Queensland**: Lloyd Bay, 3 mi N of Claudie River mouth, 25.xii.1971, D.K. McAlpine and G.A. Holloway, 37♂♂ 17♀♀; Portland Roads, 14.xii.1971, D.K. McAlpine, G.A. Holloway, and D.P. Sands, 1♂ 3♀♀. **Papua New Guinea**, Port Moresby, Ela Beach, 10.i.1964, D.K. McAlpine, 7♂♂ 5 cf. ♀♀ [AM]

Distribution. Afrotropical: Kenya, Madagascar, Seychelles (Aldabra, Astove, Mahé). South Indian Ocean Islands: Amsterdam Island. Australasian/Oceanian: Australia (QLD) [**new distribution**], Caroline Islands (Yap), Mariana Islands (Saipan), Palau, Papua New Guinea [**new distribution**]. Oriental: China (Hong Kong - Lantau), Malaysia (Sabah, Singapore), Philippines (Balabac, Busuanga, Calicoan, Culion, Leyte, Mindanao, Negros Oriental, Palawan).

Remarks. Males of this widespread species are easily distinguished from congeners by the peculiar shape of the posteroventral armature of the mid femur (see key). Conversely, the females are not so easily identifiable, since they are very similar to females of many other species.

Dasyrhicnoessa fulvescens Malloch, 1935

Mathis & Sasakawa, 1989: 667; Mathis & Munari, 1996: 12.

Distribution. Australia (QLD).

After thorough examination of the holotype preserved in AM, I am now able (see Munari, 2002) to confirm the validity of this species and dispel any doubt about a possible (see Malloch, 1935) conspecificity with *Dasyrhicnoessa serratula* Malloch. *Dasyrhicnoessa fulvescens* is chiefly characterized by the following combination of characters: body and legs entirely pale to fulvous yellow, except for syntergite 1+2 and tergite 3 broadly blackened (I do not know whether this colour is of pigmental nature or due to *postmortem* factors affecting the internal organs); all setae and setulae golden brownish or golden yellow; arista micropubescent; fore femur lacking true ctenidium, but with 3–4 microscopic, thin hairs present at its place; 4 rather regular rows of acrostichal setulae on anterior half of scutum (thus, not "irregularly sexseriate" as erroneously stated by Malloch [1935]); both proepimeral and proepisternal setae present. No other species of *Dasyrhicnoessa* share these features.

Dasyrhicnoessa humilis n.sp.

Figs. 9–10

Type material. HOLOTYPE ♂ **Australia, New South Wales**: "Careel Bay, / Avalon, NSW. / 15 Dec. 1964 / D.K. McAlpine / Mangroves // HOLOTYPUS / *Dasyrhicnoessa / humilis* sp.n. ♂ / L. Munari des." AM K186737. The specimen is in excellent condition, and is double mounted (glued on the tip of a triangular card); abdomen dissected, stored in glycerol in a small plastic tube, and pinned below the specimen. PARATYPES: **Australia, New South Wales**: same data as holotype, 3♂♂ 4♀♀; "Careel Bay / N. South Wales / 27 Oct. 1962 / Mangroves / D.K. McAlpine", 1♂; "Mangroves / Careel Bay, / Avalon, NSW. / 3 Feb. 1973 / D.K. McAlpine", 1♂; "In mangroves / North Cronulla / NSW., 1 March, 1962 / D.K. McAlpine", 1♂. **Australia, Queensland**: "Mangroves. / Gladstone, Qld. / 19 Dec. 1961 / D.K. McAlpine", 3♂♂ 6♀♀. The holotype and most of the paratypes are deposited in AM, a few paratypes are preserved in MCV.

Description. *Size*. Body length 1.7 mm (1.6–2.0), wing length 1.5 mm (1.4–1.7), wing width 0.5 mm (0.5–0.6). *Habitus*. Yellowish grey to dark grey species with setal vestiture golden brown to blackish. Wings yellowish grey. *Head*. Yellowish, with frons reddish yellow and occiput greyish yellow; frons with frontal and orbital vittae covered with whitish microtomentum, and golden yellow patches, on both sides of ocellar triangle, merging before anterior ocellus; paravertical setae well developed, strongly inclinate; inner vertical seta inwardly curved, strong, about as long as lateroclinate outer vertical seta; postocular and postgenal setae short, former ones in two irregular rows; upper postocular seta long, inclinate towards inner vertical seta; ocellar triangle bearing pair of moderately long pseudopostocellar setae in addition to pair of strong ocellars; 3 very short, thin setulae between ocellars and pseudopostocellars; 3 strong, lateroclinate orbital setae; row of thin, inclinate setulae on orbital vitta between 2 anterior orbitals and frontals; 4 short, strong, additional setulae before anterior orbital seta, between this one and anterior margin of orbital vitta; 3 pairs of frontal setae intercalated with 3 pairs of short, thin setulae, all setae and setulae inclinate, mid pair cruciate at apex; antenna with postpedicel slightly infuscated, brownish, bearing microscopically pubescent, brown arista; Eye micropubescent, large, distinctly oblong vertically, its longest diameter 5.6× as long as genal height; 7 blackish peristomal setae, 3 anterior ones, including vibrissa, long and strong; mouth parts pale yellow, with labellum stumpy, distinctly shorter than length of buccal cavity, and palpus long, slender, bearing scattered black setulae. *Thorax*. Yellowish grey; 1+3 dorsocentral setae; 6 rows of acrostichal setulae on anterior half of scutum, otherwise arranged in 4 rows; prescutellar acrostichals long; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta long and strong, anterior setae shorter and weaker; 1 very long presutural seta; 2 notopleurals about subequal in length; 1 supra-alar, below and before it four short and weak setae; 2 postalars, external one distinctly longer and stronger; scutellum with 4 long marginal setae; proepisternal seta long and strong, proepimeral one weak and slightly shorter; anepisternum with scattered setulae, bearing 3 long, posteriorly directed, posteromarginal setae, mid one distinctly longer and stronger, and 1 erect seta at posterodorsal margin; katepisternum with few scattered setulae, bearing long and strong posterodorsal seta; anepimeron, katatergite, and meron without setae and setulae. *Legs*. Evenly setulose, bearing short, blackish setae and setulae, except for foreleg having coxa with scattered, pale brownish, long setae, and femur with posterodorsal and posteroventral rows of spaced, long setae; fore femur without true ctenidium, only with single row of very short, thin, black setulae (possibly spine-like) anteroventrally on distal half; mid femur of male with row of spaced, spine-like, posteroventral black setae, decreasing in length distally; all legs, including coxae, yellow, with last tarsomere slightly infuscated. *Wing*. Veins pale brownish, membrane yellowish grey; alula with fringe formed by long, erect, blackish setae; costal vein reaching end of M_1, bearing several, spaced, microscopic setulae on both dorsal and ventral surfaces; R_{2+3} distinctly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending at basal third of cell *dm*; crossvein *dm-cu* slightly shorter than one third of last section of CuA_1; halter yellowish. *Abdomen*. Syntergite 1+2 yellowish, remaining tergites black, each of them with narrow, apicomarginal, whitish stripe; setal vestiture blackish. *Male terminalia* (Figs. 9–10). Epandrium bearing some long to very long setae on distal half, in particular on anteroapical surface, intermixed with shorter setae on entire posterior surface; cercus small, pubescent, dorsally covered with microscopic hairs and with long setae; anterior surstylus short and stumpy, bearing scattered, thin setae; posterior surstylus rather squat, bearing several long setae and apical cluster of thick tubercles on inner side; aedeagal apodeme long and straight, distinctly sclerotized on distal half; ejaculatory apodeme with well-developed distal fan; distiphallus long and slender, ribbon-like, bearing micropubescence on its basal half and subapically.

Female. Similar to male, except for slight sexual dimorphism. *Female terminalia*. Cerci long, straight, bearing scattered, thin setulae; spermathecae spherical, smooth.

Distribution. Australia (NSW, QLD).

Etymology. From the Latin *humilis* meaning poor, humble or unpretentious. The specific epithet refers to the modest habitus and size of the new species as well as to the simple morphological features of the male terminalia.

Dasyrhicnoessa insularis (Aldrich, 1931)

Munari & Evenhuis, 2000: 145–147; Munari, 2002: 546–547, 550.

Material examined. **Australia, Queensland**: Mackay, mangroves, 19.i.1967, D.K. McAlpine & G.A. Holloway, 1♂.[AM]

Distribution. Afrotropical: Cameroon, Madagascar, Nigeria. Australasian/Oceanian: American Samoa (Tutuila), Australia (QLD) [**new distribution**], Canton Island, Caroline Islands (Ponhpei, Chuuk, Yap, Palau), Fiji Islands (Ovalau, Suva [**new distribution**, see Appendix], Viti Levu), Hawaii (Hawaii, French Frigate Shoals, Hilo, Maui, Oahu, Pearl and Hermes Reef), Kiribati (Butaritari, Makin, Eita, Tarawa, Abemama), Line Islands (Christmas), Mariana Islands (Saipan, Tinian), Marquesas (Hivaoa, Nuku Hiva), Marshall Islands (Majuro, Japtan, Parry, Lib, Jibu, Jaluit, Namorik), Palmyra Island, Pitcairn Island, Rapa Island, Society Islands (Bora Bora, ?Moorea [see appendix]), Wake Island. Nearctic: Bermuda, USA (Florida). Neotropical: Bahamas (South Bimini), Belize, Brazil (Ceará), Mexico (Tabasco), West Indies (Cuba, Dominica, St. Lucia, St. Vincent).

Remarks. A pantropical species easily distinguished from congeners only by examination of the male terminalia. Females not strictly associated with males in the same biotope are not reliably identifiable.

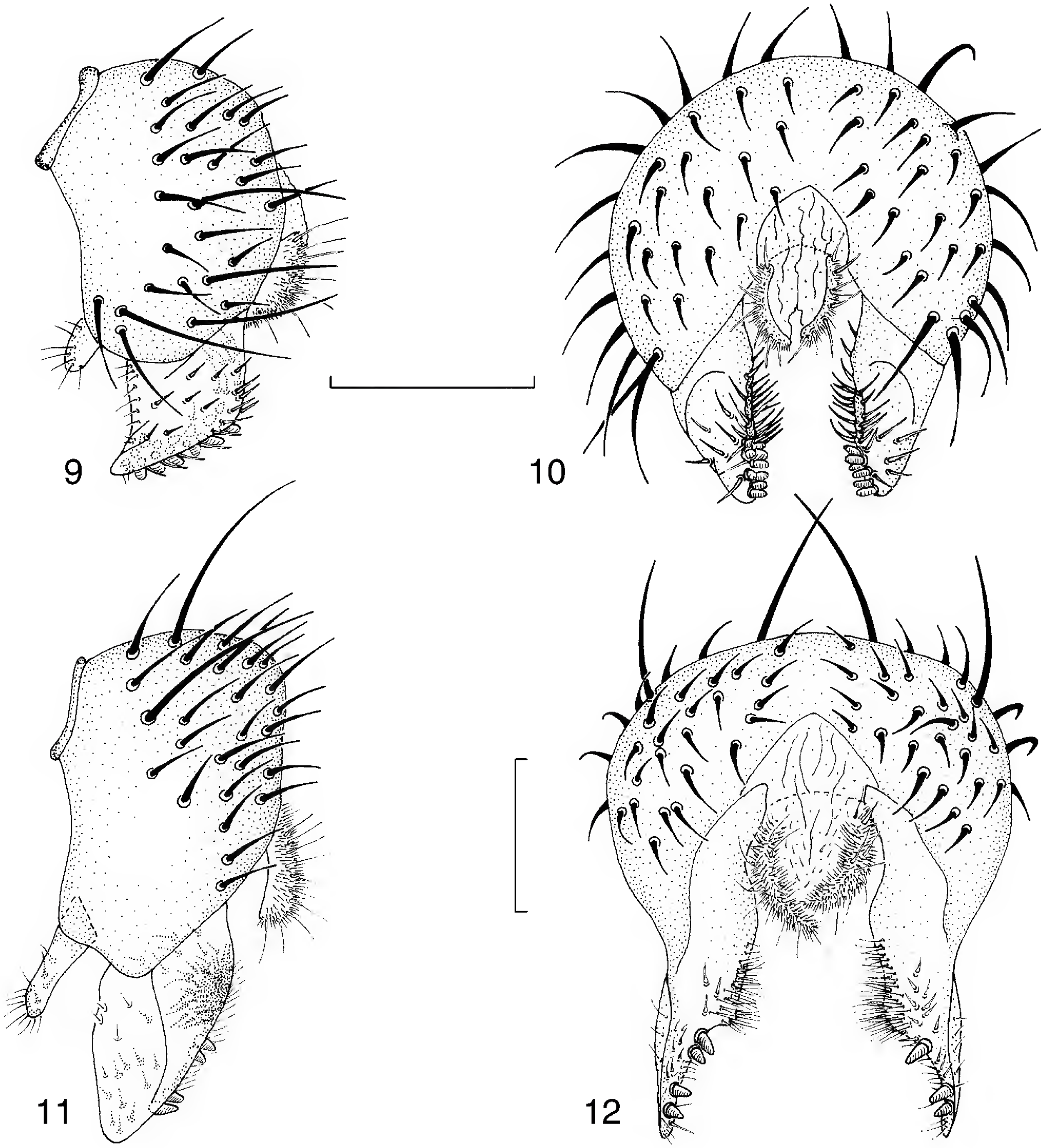
Dasyrhicnoessa longisetosa n.sp.

Figs. 11–12

Type material. HOLOTYPE ♂ **Papua New Guinea** "Mangroves, / Port Moresby, / Papua 25 Oct. 1963 / D.K. McAlpine" // "HOLOTYPUS / *Dasyrhicnoessa* / *longisetosa* sp.n. ♂ / L. Munari des." AM K186738. The specimen is in excellent condition, and is double mounted (glued on the tip of a triangular card); abdomen dissected, stored in glycerol in a small plastic tube, and pinned below the specimen. PARATYPES **Australia, Queensland**: "Mangroves, / Gladstone, Qld. / 19 Dec. 1961 / D.K. McAlpine", 1♂; "Mangroves. / Mackay, Q. / 19 Jan. 1967 // D. McAlpine & / G. Holloway coll.", 4♂♂ 11♀♀. The holotype and most of the paratypes are deposited in AM, a few paratypes are preserved in MCV.

Distinguishing features. The new species is closely related to both *D. ciliata* n.sp. and *D. priapus* n.sp., in particular to the latter species, differing from them noticeably in the morphology of the male terminalia.

Description. *Size*. Body length 2.0 mm (2.0–3.1), wing length 1.8 mm (1.8–2.6), wing width 0.6 mm (0.6–1.0). *Habitus*. Yellow species with setal vestiture golden brown. Setae of mesonotum longer than ones of congeners. Head yellow with antenna bearing long-haired arista. Wings yellowish grey. *Head*. Entirely yellow; frons, including orbital vittae, homogeneously yellow, except for usual golden yellow patch on both sides of ocellar triangle; paravertical setae well developed, inclinate; inner vertical seta inwardly curved, strong, about as long as or slightly longer than lateroclinate outer vertical seta; postocular and postgenal setae somewhat long, former ones in single row; upper postocular seta long and strong, inclinate towards inner vertical seta; ocellar triangle bearing pair of long, thin pseudopostocellar setae in addition to pair of strong ocellars; 2–3 very short, thin setulae between ocellars and pseudopostocellars; 3 strong, lateroclinate orbital setae; row of long, thin, inclinate setulae on orbital vitta between two anterior orbitals and frontals; 3 pairs of frontal setae plus 2 pairs of thin setulae, all setae and setulae inclinate, two anterior frontal setae cruciate at apex; antenna with large and pubescent postpedicel, bearing blackish, long-haired arista (an apomorphic character state); eye micropubescent, very large, slightly oblong vertically, its longest diameter 7.7× as long as genal height; 6 dark brown peristomal setae decreasing in length and strength from front to back; vibrissal seta long and strong; mouth parts pale yellow, with labellum as long as or slightly shorter than length of buccal cavity, and palpus long, slightly clavate, bearing scattered black setulae. *Thorax*. Entirely yellowish, with mesonotum slightly darker than pleura; 1+3 very long dorsocentral setae; 5–6 rows of acrostichal setulae on anterior half of scutum, otherwise arranged in 4 rows; prescutellar acrostichals very long and strong; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta long and strong, anterior setae shorter and slightly weaker; 1 long presutural seta; 2 notopleurals about subequal in length; 1 supra-alar, below and before it two shorter and weaker setae; 2 postalars, external one distinctly longer and stronger; scutellum with 4 long marginal setae; both proepisternal and proepimeral setae present; anepisternum with scattered setulae, bearing 3 long, posteriorly directed, posteromarginal setae, mid one longer and stronger, and 1 erect seta at posterodorsal margin; katepisternum with few scattered setulae, bearing long and strong posterodorsal seta; anepimeron, katatergite, and meron without setae and setulae. *Legs*. Evenly setulose, bearing short, yellowish to brownish yellow setae and setulae, except for foreleg having coxa with long setae, and femur with a few posterodorsal and posteroventral setae; fore femur without true ctenidium, only with short row of thin setulae anteroventrally at distal third; mid femur of male with row of posteroventral, spine-like, long, spaced, black setae on distal half; all legs, including coxae, yellow, with last tarsomere very slightly infuscated. *Wing*. Veins yellowish, membrane yellowish grey; alula with fringe formed by long, erect, diaphanous setae; costal vein reaching end of M_1, bearing several, spaced, microscopic setulae on dorsal and ventral surfaces; R_{2+3} slightly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending before middle of cell *dm*; crossvein *dm-cu* distinctly shorter than half of last section of CuA_1; halter yellowish. *Abdomen*. Mostly yellowish, with setal vestiture formed by golden brown setulae and darker posteromarginal setae on each tergite; transverse stripes at posterior edge of tergites yellow, hardly discernible. *Male terminalia* (Figs. 11–12). Epandrium bearing two pairs of long setae dorsally, and several short setae on remaining posterior surface; cercus of normal size, pubescent, dorsally covered with microscopic hairs and with long, thin setae; anterior surstylus simple, straight, bearing sparse, thin setae on inner side; posterior surstylus almond-shaped in lateral view, narrow and pointed in posterior view, bearing few stout tubercles on posterior margin of distal half



Figs. 9–12. Terminalia of male. *Dasyrhicnoessa humilis* n.sp.: (9) lateral view, (10) posterior view. *Dasyrhicnoessa longisetosa* n.sp.: (11) lateral view, (12) posterior view. Scale bars: 0.1 mm.

and characteristic cluster of thin setae on posterior margin of mid surface; aedeagal apodeme straight to slightly bisinuate; ejaculatory apodeme large, as long as or slightly shorter than aedeagal apodeme, with distal fan broad, well developed; distiphallus long, ribbon-like, with ventral micropubescence on basal half as well as subapically; marginal, membranous, aedeagal lobe distinctly visible medially.

Female. Similar to male, except for slight sexual dimorphism. *Female terminalia*. Cerci long, straight, bearing several thin setulae; spermathecae spherical, smooth.

Distribution. Australia (QLD), Papua New Guinea.

Remarks. Apart from the various, often considerable, morphological features of the body and male terminalia, the new species is recognizable by having the mesonotal setae distinctly longer than those of congeners.

Etymology. Compound word, from the Latin *longus* meaning long, and *saetosus* meaning bearing setae or bristly. The specific epithet refers to the relatively long setae of the head and thorax.

Dasyrhicnoessa macalpinei n.sp.

Figs. 13–14

Type material. HOLOTYPE ♂ **Australia, Northern Territory** "NT: Buffalo Ck, / Darwin; 2–5 Mar. / 1996; D.K. McAlpine, / G.R. Brown // HOLOTYPUS / *Dasyrhicnoessa / mcalpinei* sp.n. ♂ / L. Munari des." AM K186739. The specimen is in relatively good condition: the left fore tibia and tarsus are missing, and the head is glued near the specimen. The holotype is deposited in AM, and is double mounted (glued on the tip of a triangular card label); abdomen dissected, stored in glycerol in a small plastic tube, and pinned below the specimen.

Description. *Size*. Body length 1.3 mm, wing length 1.3 mm, wing width 0.5 mm. *Habitus*. Small fly with body and legs pale yellowish. Setal vestiture pale yellow to dark brownish. Wings yellowish grey. *Head*. Yellowish to greyish yellow; frontal and orbital vittae pale yellow, distinctly paler than rest of frons; ocellar triangle and occiput greyish; golden yellow patch on both sides of ocellar triangle; paravertical setae thin, strongly inclinate; inner vertical seta inwardly curved, strong, about as long as lateroclinate outer vertical seta; postocular and postgenal setae very short, thin, former setae in 1–2 irregular rows; upper postocular seta long, inclinate towards inner vertical seta; ocellar triangle bearing pair of moderately long, thin pseudopostocellar setae in addition to pair of strong ocellars; a few very short, thin setulae between ocellars and pseudopostocellars, and behind latter setae; 3 strong, lateroclinate orbital setae intermixed with sparse, thin, short setulae; 3 pairs of frontal setae intercalated with 3 pairs of short, thin setulae, all setae and setulae inclinate; antennal postpedicel bearing brownish, short-haired arista; eye micropubescent, very large, slightly oblique, subrectangular, its longest diameter 5.5× as long as genal height; 5 brownish to black peristomal setae, two anterior ones, including vibrissa, long and strong; mouth parts pale yellow, with labellum stumpy, shorter than length of buccal cavity, and palpus long, slender, bearing scattered black setulae. *Thorax*. Yellowish; 1+3 dorsocentral setae; acrostichal setulae in 4 irregular rows; prescutellar acrostichals long; postpronotal lobe bearing 3 setae (only two are discernible in holotype, lower seta being missing), each with different inclination, posterior seta long and strong, anterior setae shorter and weaker; 1 long presutural seta; 2 notopleurals, anterior one slightly longer; 1 supra-alar (missing in holotype), below it 1 shorter and weaker seta; 2 postalars, external one distinctly longer and stronger; scutellum with 4 long marginal setae; both proepisternal and proepimeral setae present; anepisternum with scattered setulae, bearing 3 long, posteriorly directed, posteromarginal setae, mid one distinctly longer and stronger, and 1 erect seta at posterodorsal margin; katepisternum with few scattered setulae, bearing long and strong posterodorsal seta; anepimeron, katatergite, and meron without setae and setulae. *Legs*. Evenly setulose, bearing short brownish to blackish setae and setulae, except for foreleg having coxa with scattered, pale brownish, long setae, and femur with posterodorsal and posteroventral rows of spaced, long setae; hind tibia with long, posteroventral pubescence on distal half, formed by several, erect, yellowish setae; fore femur without true ctenidium, only with row of short, thin setulae anteroventrally on distal half; mid femur with comb of 6 spine-like, short, subequal in length, posteroventral black setae on distal half; all legs, including coxae, yellow; last tarsomere slightly infuscate. *Wing*. Veins yellowish, membrane yellowish grey; alula with fringe formed by erect, blackish setae; costal vein reaching end of M_1, bearing several, spaced, microscopic setulae on both dorsal and ventral surfaces; R_{2+3} distinctly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending just before middle of cell *dm*; crossvein *dm-cu* distinctly shorter than half of last section of CuA_1; halter yellow. *Abdomen*. Yellowish brown, with setal vestiture formed by golden brown setae and setulae; transverse stripes at posterior edge of tergites yellowish. *Male terminalia* (Figs. 13–14). Epandrium bearing characteristic cluster of long, strong setae on entire anteroventral surface, in particular on anterior part, and short setae on all remaining posterior surface; cercus long and narrow, pointed apically, pubescent, dorsally covered with microscopic hairs and with long setae; anterior surstylus strongly reduced, rounded at apex, bearing scattered, thin setae; posterior surstylus subrectangular in lateral view, long, straight, and narrow in posterior view, bearing numerous short setae and cluster of short, stout tubercles on distal third; aedeagal apodeme long and straight, without evident sinuosity; ejaculatory apodeme diaphanous, poorly sclerotized, with distal fan well developed; distiphallus long, slender, ribbon-like, distinctly pointed at apex, bearing several, scattered, microscopic hairs.

Female. Unknown.

Distribution. Australia (NT).

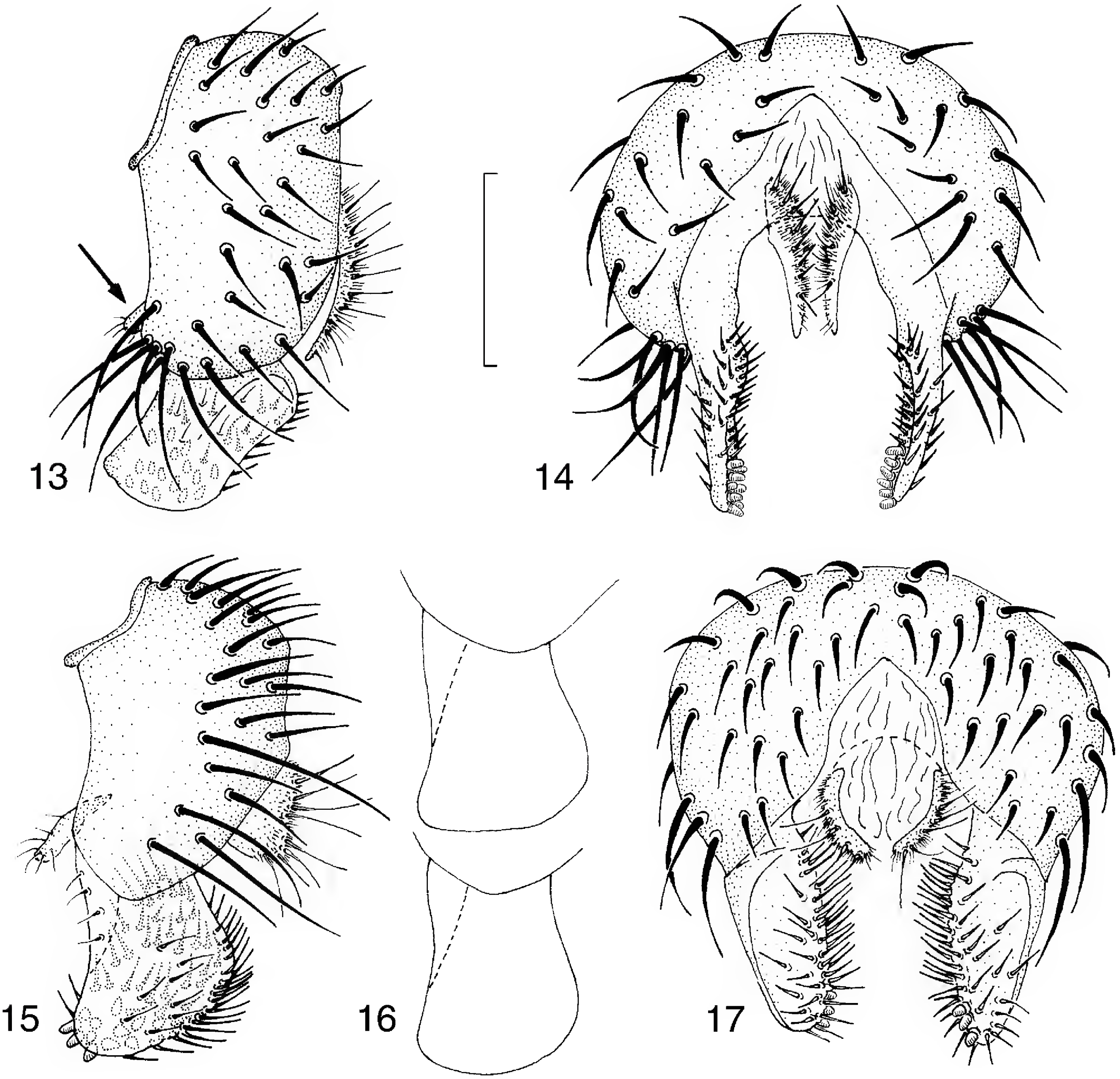
Remarks. As regards the external morphology, the new species is particularly characterized by having the hind tibia of the male bearing long, thin, yellowish pubescence on the posteroventral distal half. Personally, I have never observed this character in any other *Dasyrhicnoessa* species. It would be interesting to know whether the females also share such a peculiar feature.

Etymology. The new species is gratefully named after Dr David K. McAlpine who collected the holotype and facilitated my study of a large number of specimens held at the Australian Museum.

Dasyrhicnoessa ostentatrix n.sp.

Figs. 15–17

Type material. HOLOTYPE ♂ **Australia, New South Wales** "Swept Sea grass / Careel Bay, / Avalon, NSW. // 12 May 1984 / D.K. McAlpine / D.J. Bickel // HOLOTYPUS / *Dasyrhicnoessa / ostentatrix* sp.n. ♂ / L. Munari des." AM K186740. The specimen is in excellent condition, and is double mounted (glued on the tip of a triangular card); abdomen dissected, stored in glycerol in a small plastic tube, and pinned below the specimen. PARATYPES (many specimens were prepared by AM technicians using the *brochette* double mounting method): **Australia, New South Wales**: same data as holotype, 45♂♂ 28♀♀; "NSW: Broken Head / nr Byron Bay / 7–8 Nov. 2000 // Shoreline rocks / D.K. McAlpine", 3♂♂ 2♀♀; "Bundagen, via Repton / NSW 15 Jan. 1971 / D.K. McAlpine / & A. Hughes // MV lamp", 1♂; "Careel Bay / N. South Wales / 27 Oct. 1962 // Mangroves / D.K. McAlpine", 3♂♂ 11♀♀; *ibidem*,



Figs. 13–17. Terminalia of male. *Dasyrhicnoessa macalpinei* n.sp.: (13) lateral view (the arrow indicates the small anterior surstylus), (14) posterior view. *Dasyrhicnoessa ostentatrix* n.sp.: (15) lateral view, (16) posterior surstylus outline variability, (17) posterior view. Scale bar: 0.1 mm.

"14 March 1963 // on beach / D.K. McAlpine", 1♂; "Careel Bay, / Avalon, NSW. / 15 Dec. 1964 // Mangroves", 1♂ 1♀; 14 June 1965, on beach, 5♂♂ 5♀♀; 8 Nov 1975, 39♂♂ 25♀♀; "Glenfield, near / Sydney, NSW / 2 April 1967 [or 1957?] // D.J. Lee / collector", 1♂; "Little Beach nr / Terrigal, NSW / 29 Jan. 1988 // On beach / D.K. McAlpine / and B.J. Day", 1♂; "Tidal flat, / Merimbula, NSW. / 12 Febr. 1963. / D.K. McAlpine", 6♂♂ 2♀♀; "North Creek, near / Ballina, NSW / 1 March 1965 / McAlpine & Lossin", 4♂♂ 10♀♀; "Mangroves, Nth / Cronulla, NSW. / 21 Jan. 1962 / D.K. McAlpine", 11♂♂ 13♀♀; 29 Jan. 1962, 62♂♂ 58♀♀; 1 March 1962, 7♂♂; 31 March 1972, 43♂♂ 45♀♀. **Australia, Victoria**: "Bunarong Cliffs 5 km / SW Inverloch, Vic. / 8 Apr. 1986 / D.K. McAlpine // On stranded kelp", 1♂. The holotype and most of the paratypes are deposited in AM, some paratypes are preserved in MCV.

Description. *Size*. Body length 1.8 mm (1.2–2.1), wing length 1.8 mm (1.5–1.9), wing width 0.6 mm (0.5–0.6). *Habitus*. Dark grey to ochreous yellow species, with setal vestiture dark brown to black. Wings yellowish grey. *Head*. Frons brownish yellow, with frontal and orbital vittae pale yellowish, and with golden brown patch on both sides of dark grey ocellar triangle, latter concolorous with postcranium; antennal postpedicel infuscated; face, parafacial, and gena pale yellow; gena with distinct, longitudinal, narrow, translucent stripe as in many species of *Tethina* Haliday; paravertical setae long and thin; inner vertical seta inclinate, strong, about as long as lateroclinate outer vertical seta; postocular and postgenal setae short, former ones in 1–2 irregular rows; upper postocular seta long, inclinate towards inner vertical seta; ocellar triangle bearing pair of moderately long pseudopostocellar setae in addition to pair of strong ocellars; few short, thin setulae between ocellars and pseudopostocellars; 3 strong, lateroclinate orbital setae; row of thin, inclinate setulae on orbital vitta between two anterior orbitals and frontals; 3–4 short, additional setulae before anterior orbital seta, between this one and anterior margin of orbital vitta; 3 pairs of frontal setae intercalated with 3–4 pairs of short, thin setulae, all setae and setulae inclinate; antenna with brownish postpedicel, bearing short-haired, black arista; eye micropubescent, large, oblique, its longest diameter 5.2× as long as genal height; 6–7 black peristomal setae, three anterior ones, including vibrissa, long and strong; mouth parts pale yellowish, with labellum slightly shorter than length of buccal cavity; palpus long, slender, bearing scattered black setulae. *Thorax*. Dark grey to ochreous; 1+3 dorsocentral setae; 6 rows of acrostichal setulae on anterior half of scutum, otherwise arranged in 4 rows; prescutellar acrostichals long and strong; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta long and strong, anterior setae shorter and weaker; 1 long presutural seta; 2 notopleurals about subequal in length; 1 supra-alar, below it 1 short seta; 2 postalars, external one distinctly longer and stronger; scutellum with 4 long marginal setae; both proepisternal and proepimeral setae present; anepisternum with few, scattered setulae (more numerous in most paratypes), bearing 3 long, posteriorly directed, posteromarginal setae, mid one distinctly longer and stronger, and 1 erect seta at posterodorsal margin; katepisternum with few, scattered setulae, bearing long and strong posterodorsal seta; anepimeron, katatergite, and meron without setae and setulae. *Legs*. Evenly setulose, bearing short, blackish setae and setulae, except for foreleg having coxa with scattered, black, long setae, and femur with posterodorsal and posteroventral rows of spaced, long, strong setae; ctenidium of fore femur formed by few (4 in holotype), weak, short, spinulae; mid femur of male with long row of spaced, spine-like, posteroventral black setae, decreasing in length distally; all legs, including coxae, yellowish grey; last two tarsomeres slightly infuscated. *Wing*. Veins pale brownish, membrane yellowish grey to grey; alula with fringe formed by long, erect, blackish setae; costal vein reaching end of M_1, bearing several, spaced, microscopic setulae on both dorsal and ventral surfaces; R_{2+3} distinctly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending on basal third of cell *dm*; crossvein *dm-cu* slightly shorter than one third of last section of CuA_1; halter yellowish. *Abdomen*. Dark brown to blackish, with tergites showing very narrow, apicomarginal, yellowish stripes; setal vestiture blackish. *Male terminalia* (Figs. 15–17). Epandrium bearing long and strong setae on distal half, and several shorter setae on all remaining posterior surface; cercus of normal size, pubescent, dorsally covered with microscopic hairs and with long setae; anterior surstylus very small, slightly bent medially, bearing sparse, thin setae; posterior surstylus lobe-shaped, with lateral profile variable in many paratypes (Figs. 15–16), bearing several long setae and apical cluster of stout tubercles on inner side; aedeagal apodeme long, straight, only slightly bent distally; ejaculatory apodeme with distal fan well developed, more or less sclerotized; distiphallus long, ribbon-like, micropubescent.

Female. Similar to male, except for slight sexual dimorphism. *Female terminalia*. Cerci moderately long, setulose; spermathecae spherical, smooth.

Distribution. Australia (NSW, VIC).

Remarks. The new species shows a marked variability in coloration, with individuals having dark grey to ochreous yellow thorax, and with dark brown to black setal vestiture. That implies a considerable degree of difficulty in identifying the female specimens, unless they are strictly associated with several male specimens from the same biotope. In the preserved material, the males are easily distinguished from congeners in having the abdomen, when observed laterally, with the posterior surstyli distinctly and characteristically exposed outwards. Also, the lateral outline of the surstylus often exhibits a fair variability (Figs. 15–16).

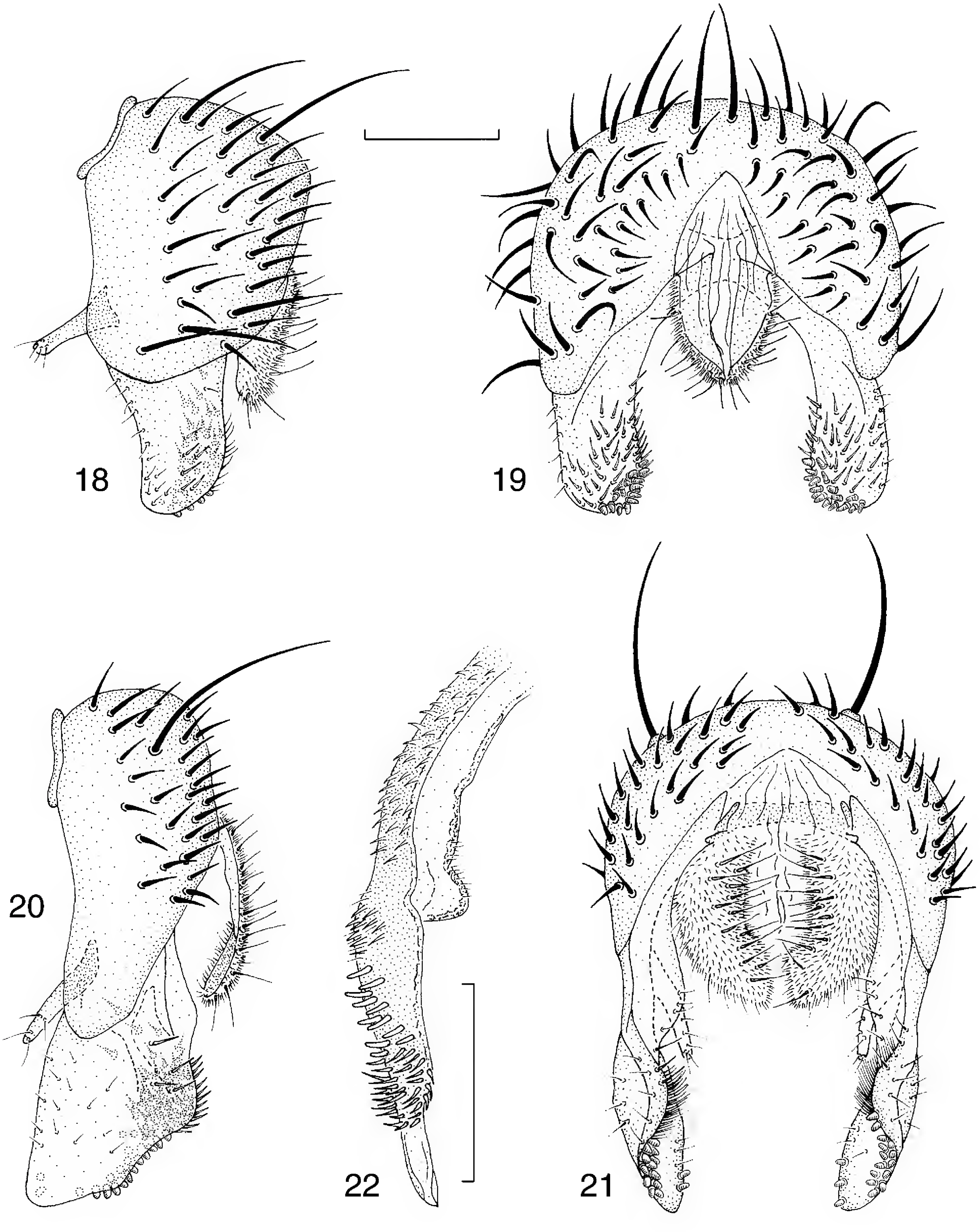
Etymology. From the Latin *ostentatrix* meaning exhibitionist, parading or showing. The specific epithet refers to the external male terminalia which are distinctly exposed outwards.

Dasyrhicnoessa pallida n.sp.

Figs. 18–19

Type material. HOLOTYPE ♂ **Australia, Queensland** "Mangroves. / Mackay, Q. / 19 Jan. 1967. // D. McAlpine & / G. Holloway coll. // HOLOTYPUS / *Dasyrhicnoessa / pallida* sp.n. ♂ / L. Munari des." AM K186741. The specimen is in excellent condition, and is double mounted (glued on the tip of a triangular card); abdomen dissected, stored in glycerol in a small plastic tube, and pinned below the specimen. PARATYPES **Australia, Queensland**: same data as holotype, 2♂♂ 6♀♀. The holotype and most of the paratypes are deposited in AM, a couple of paratypes are preserved in MCV.

Description. *Size*. Body length 2.2 mm (2.1–2.5), wing length 1.8 mm (1.7–2.0), wing width 0.7 mm (0.6–0.8). *Habitus*. Yellowish to greyish yellow species with setal vestiture dark brown to blackish. Wings yellowish grey. *Head*. Yellow, except for frons reddish yellow having orbital vittae distinctly lighter and usual golden yellow patch on both sides of ocellar triangle; paravertical setae well developed, thin, inclinate; inner vertical seta inclinate, strong, about as long as lateroclinate outer vertical seta; postocular and postgenal setae short, former ones in single row; upper postocular seta long, inclinate towards inner vertical seta. Ocellar triangle bearing pair of moderately long, thin pseudopostocellar setae in addition to pair of strong ocellars; a few very short, thin setulae between ocellars and pseudopostocellars; 3 strong, lateroclinate orbital setae; row of thin, inclinate setulae on orbital vitta between two anterior orbitals and frontals; 6 short, strong, additional setulae before anterior orbital seta, between this one and anterior margin of orbital vitta; 3 pairs of frontal setae intercalated with 3 pairs of short, thin setulae, all setae and setulae inclinate, frontal setae often cruciate at apex. Antenna with large and pubescent postpedicel, bearing blackish, microscopically pubescent arista. Eye micropubescent, large, slightly oblong vertically, its longest diameter



Figs. 18–22. Terminalia of male. *Dasyrhicnoessa pallida* n.sp.: (18) lateral view, (19) posterior view. *Dasyrhicnoessa priapus* n.sp.: (20) lateral view, (21) posterior view, (22) apex of distiphallus. Scale bars: 0.1 mm.

4.6× as long as genal height; 6 blackish peristomal setae, three anterior ones, including vibrissa, long and strong. Mouth parts pale yellow, with labellum stumpy, shorter than length of buccal cavity, and palpus long, slightly clavate, bearing scattered black setulae. *Thorax*. Yellowish with scutum greyish, slightly darker than pleura and scutellum; 1+3 dorsocentral setae; 6 irregular rows of acrostichal setulae on anterior half of scutum, otherwise arranged in 4 rows; prescutellar acrostichals long and strong; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta long and strong, anterior setae shorter and weaker; 1 long presutural seta; 2 notopleurals about subequal in length; 1 supra-alar, below and before it 2–3 short and weaker setae; 2 postalars, external one distinctly longer and stronger; scutellum with 4 long marginal setae; proepisternal seta long and strong, proepimeral one weak and slightly shorter; anepisternum with scattered setulae, bearing 2–3 long, posteriorly directed, posteromarginal setae, mid one distinctly longer and stronger, and 1 erect seta at posterodorsal margin; katepisternum with few scattered setulae, bearing long and strong posterodorsal seta; anepimeron, katatergite, and meron without setae and setulae. *Legs*. Evenly setulose, bearing short blackish setae and setulae, except for foreleg having coxa with few pale brownish to black long setae, and femur with posterodorsal and posteroventral rows of spaced, long setae; fore femur without true ctenidium, only with simple row of very short, thin setulae anteroventrally on distal half; mid femur of male with posteroventral comb of spine-like, short, subequal in length, slightly but distinctly curved forward, black setae on distal half. All legs, including coxae, yellow; last tarsomere not or indistinctly infuscated. *Wing*. Veins yellowish, membrane yellowish grey; alula with fringe formed by long, erect, blackish setae; Costal vein reaching end of M_1, bearing several, spaced, microscopic setulae on both dorsal and ventral surfaces; R_{2+3} distinctly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending before middle of cell *dm*; crossvein *dm-cu* distinctly shorter than one third of last section of CuA_1; halter yellow. *Abdomen*. Mostly yellowish to brownish yellow, with median, longitudinal, brown stripe, and setal vestiture formed by golden brown setae and setulae; transverse stripes at posterior edge of tergites yellow, hardly discernible. *Male terminalia* (Figs. 18–19). Epandrium bearing some long setae dorsally and ventrolaterally, and several short setae on all remaining posterior surface; cercus of normal size, dorsally covered with microscopic hairs and with long setae; anterior surstylus short, straight, narrow, bearing few apical, thin setae; posterior surstylus lobe-shaped, distinctly squat in caudal view, bearing many short setae and apical cluster of stout tubercles on inner side; aedeagal apodeme long and straight; ejaculatory apodeme stumpy, with distal fan moderately though distinctly developed; distiphallus long and slender, ribbon-like, with evident micropubescence on basal half as well as subapically.

Female. Similar to male, except for slight sexual dimorphism. *Female terminalia*. Cerci long, straight, bearing thin setulae dorsally and apically; spermathecae spherical to subspherical, in a few paratypes with chitinous wall surrounding spermathecal duct opening distinctly invaginated (possibly collapsed).

Distribution. Australia (QLD).

Remarks. In this species the lateral profile of the male terminalia vaguely resembles that of *Dasyrhicnoessa mathisi* Munari even though the latter species has the anterior surstylus noticeably longer and stouter. Additionally, the two species are easily separable by the different colour of the body and legs.

Etymology. From the Latin *pallidus* meaning pale. The specific epithet refers to the pale hue of the body in this new species.

Dasyrhicnoessa priapus n.sp.

Figs. 20–22

Type material. HOLOTYPE ♂ **Australia, Queensland** "Mangroves / Eurimbula, Qld. / 28 Mar. 1975 / D.K. McAlpine // HOLOTYPUS / *Dasyrhicnoessa* / *priapus* sp.n. ♂ / L. Munari des." AM K186742. The specimen is in relatively good condition: head, thorax, wings, and forelegs are very well preserved (including setal vestiture), but, unfortunately, the hind legs are missing, the left mid leg is glued near the specimen, the right mid leg has both tibia and tarsus missing, and the surviving femur is broken medially. The specimen is double mounted (glued on the tip of a triangular card); abdomen dissected, stored in glycerol in a small plastic tube, and pinned below the specimen. PARATYPE: same data as holotype, 1♀. Holotype and paratype are deposited in AM.

Description. *Size*. Body length 2.2 mm (3.0), wing length 1.9 mm (2.6), wing width 0.7 mm (0.9). *Habitus*. Yellowish species with setal vestiture dark brown having golden reflections. Head yellow with antenna bearing long-haired arista. Wings yellowish grey. *Head*. Entirely yellow; frons, including orbital vittae, homogeneously yellow, except for usual, golden yellow patch on both sides of ocellar triangle; paravertical setae very long and rather strong, inclinate; inner vertical seta inwardly curved, strong, about as long as lateroclinate outer vertical seta; postocular and postgenal setae somewhat long, former ones very distinctive and in single row; upper postocular seta long and strong, inclinate towards inner vertical seta; ocellar triangle bearing pair of long pseudopostocellar setae in addition to pair of strong ocellars; two very short, thin setulae between ocellars and pseudopostocellars; 3 very strong, lateroclinate orbital setae; a few long, thin setulae on orbital vitta in addition to orbital setae; 3 pairs of frontal setae plus 2 pairs of thin setulae, all setae and setulae inclinate, former ones cruciate at apex; antenna with large and pubescent postpedicel, bearing dark brown, long-haired arista; eye micropubescent, very large, slightly oblong vertically, its longest diameter 6.6× as long as genal height; parafacial very narrow, as a consequence vibrissal angle distinctly protruding; anterior margin of gena distinctly curved upwards, bearing three strong peristomal setae (including vibrissa); 5 dark brown peristomal setae decreasing in length and strength from front to back; vibrissal seta very long and strong; mouth parts pale yellow, with labellum distinctly shorter than length of buccal cavity; palpus long, slightly clavate, bearing scattered black setulae. *Thorax*. Entirely yellowish, with mesonotum slightly darker than pleura; 1+3 long dorsocentral setae; 6 rows of acrostichal setulae on anterior half of scutum, otherwise arranged in 4 rows; prescutellar acrostichals very long and strong; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta long and strong, anterior setae shorter and slightly weaker; 1 long presutural seta; 2 notopleurals about subequal in length; 1 supra-alar, below and before it 2 shorter and weaker setae; 2 postalars, external one distinctly longer and stronger; scutellum with 4 long marginal setae; both proepisternal and proepimeral setae present; anepisternum with scattered pubescence, bearing 2–3 long, posteriorly directed, posteromarginal setae, mid one (missing in holotype) longer and stronger, and 1 erect seta (missing in holotype) at posterodorsal margin;

katepisternum with scattered pubescence on anterior part, bearing long and strong posterodorsal seta; anepimeron, katatergite, and meron without setae and setulae. *Legs*. (In holotype the hind legs and the tibia and tarsus of the right mid leg are missing, the left mid leg is glued near the specimen) Evenly setulose, bearing short black setae and setulae, except for foreleg having coxa with very long setae, and femur with posterodorsal and posteroventral setae; fore femur without true ctenidium, only with long row of thin setulae; mid femur of male with posteroventral armature formed by spine-like, very long and spaced setae on distal half; legs, including coxae, yellow; tarsi entirely yellowish. *Wing*. Veins yellowish brown, membrane yellowish grey; alula with fringe formed by very long, erect, diaphanous setae; costal vein reaching end of M_1, bearing several, spaced, microscopic setulae on dorsal and ventral surfaces; R_{2+3} slightly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending at basal third of cell *dm*; crossvein *dm-cu* distinctly shorter than half of last section of CuA_1; halter yellowish, slightly infuscate on outer surface. *Abdomen*. Mostly yellowish, with setal vestiture formed by dark setulae and blackish posteromarginal setae on each tergite; transverse stripes at posterior edge of tergites yellowish, hardly discernible. *Male terminalia* (Figs. 20–22). Epandrium unusually long and narrow in lateral view, tapered on distal half, bearing pair of very long setae dorsally, and several short setae on remaining posterior surface; cercus very large, pubescent, covered with microscopic hairs and with long setae dorsally; anterior surstylus small and narrow, very slightly sinuous, bearing few, thin setae; posterior surstylus very large, of peculiar shape (Figs. 20–21), bearing characteristic cluster of several, thin setae as well as numerous stout tubercles on posteromarginal inner surface, 2–3 of such tubercles also present on subapical anterior inner side; aedeagal apodeme long, sinuous at basal half, slightly bent apically; ejaculatory apodeme diaphanous, with broad apical fan; distiphallus (Fig. 22) long, ribbon-like, bearing several, short, spine-like papillae on basal half, and cluster of numerous, more or less pointed, papillae subapically; ventral membranous lobe distinctly visible before apex of distiphallus.

Female. Unknown.

Distribution. Australia (QLD).

Etymology. From the Latin *Priapus* or *Priapos*, a god from classical mythology, represented by a creature having a misshapened subhuman body endowed with an enormous phallus. The specific epithet refers to the large surstyli of the male terminalia in the new species.

Dasyrhicnoessa serratula Malloch, 1935, sp.inq.

Mathis & Sasakawa, 1989: 667; Mathis & Munari, 1996: 12; Munari, 2002: 550.

Distribution. Australia (QLD).

After examining Malloch's holotype labelled "Townsville / Queensland / col. by J. Claffy // *Dasyrhicnoessa / serratula* / Type / det. JRMALLOCH // SPHTM / Coll.", I have come to the conclusion that the nomenclatural status of this species remains unresolved (Munari, 2002), as the holotype is female and no male specimen is known, and the species of *Dasyrhicnoessa* are distinguished primarily by structures of the male terminalia. Considering the external morphology and colour of this species as well as its chaetotaxy, including the presence of a strong ctenidial comb on entire distal half of the fore femur, I have not found any consistent character that could safely bring *D. serratula* near any species. It shares a very similar habitus and identical chaetotaxy with various other congeners. Thus, I here consider Malloch's species as *species inquirenda*.

Also, it should be stressed that in most *Dasyrhicnoessa* species there is no consistent external character useful for identification. The colour of the body and legs generally shows considerable variability. On male specimens it is possible to evaluate the consistency of the chaetotactic pattern of the mid femur posteroventral armature as well as, obviously, to study the morphology of the terminalia, the latter being always distinctive. Therefore, considering the range of variability that occurs in the species of *Dasyrhicnoessa* from the Indo-Pacific area, it would be irresponsible to associate a given male specimen to this unresolved species.

Dasyrhicnoessa sexseriata (Hendel, 1913)

Mathis & Sasakawa, 1989: 668; Mathis & Munari, 1996: 12; Munari, 2002: 548, 550.

Material examined. **Australia, Queensland**: Bowen, on beach, 28.xii.1966, D.K. McAlpine & G.A. Holloway, 1♂ 1♀; Mackay, mangroves, 19.i.1967, D.K. McAlpine & G.A. Holloway, 3♂♂ 1♀. **Papua New Guinea**, Port Moresby, mangroves, 25.x.1963, D.K. McAlpine, 1♂.

Distribution. Australasian/Oceanian: Australia (QLD) [**new distribution**], Caroline Islands (Yap, Palau, Pohnpei, Ponape), Fiji Islands (Ovalau, Viti Levu), Mariana Islands (Guam, Saipan), Marshall Islands (Namorik), Papua New Guinea [**new distribution**], Wake Island. Oriental: China (Hong Kong), Philippines, Taiwan.

Remarks. This species is easily distinguished from most congeners by the distinctive male terminalia.

Dasyrhicnoessa tripunctata Sasakawa, 1974

Mathis & Munari, 1996: 12; Munari, 2002: 548, 550.

Material examined. **Australia, Queensland**: Gladstone, mangroves, 19.xii.1961, D.K. McAlpine, 1♀. **Papua New Guinea**, Oro Bay, Northern Dist., 9.xii.1972, G.A. Holloway, 2♀♀; Port Moresby, mangroves, 25.x.1963, D.K. McAlpine, 1♂ 1♀.

Distribution. Australasian/Oceanian: Australia (QLD) [**new distribution**], Caroline Islands (Kosrae, Palau, Pohnpei), Mariana Islands (Guam), Papua New Guinea [**new distribution**]. Oriental: Japan (Ryukyus), Malaysia (Sabah, Sarawak), Philippines (Culion, Palawan).

Remarks. With its characteristically patterned abdomen (see key), *Dasyrhicnoessa tripunctata* is the most easily distinguishable species among all congeners.

Dasyrhicnoessa vockerothi Hardy & Delfinado, 1980

Mathis & Sasakawa, 1989: 667; Mathis & Munari, 1996: 12–13; Munari, 2002: 548, 550.

Material examined. **Australia, New South Wales**: Lord Howe I., North Bay, on beach, 21.ii.1971, D.K. McAlpine, 12♂♂ 3♀♀; *ibidem*, 24.ii.1971, 8♂♂ 6♀♀; **Australia, Northern Territory**: Smith Point, Cobourg Pen., 5.iii.1996, D.K. McAlpine, 38♂♂ 14♀♀. **Australia, Queensland**: Lloyd Bay, 3 mi N of Claudie River mouth, on beach, 25.xii.1971, D.K. McAlpine and G.A. Holloway, 1♂. **Papua New Guinea**, Port Moresby, Ela Beach, 6.x.1963, D.K. McAlpine, 4♂♂; *ibidem*, 16.x.1963, D.K. McAlpine, 3♂♂ 2 (cf.) ♀♀.[AM]

Distribution. Afrotropical: Seychelles (Aldabra, Mahé). Australasian/Oceanian: Australia (NSW, NT, QLD) [**new distribution**], Caroline Islands (Truk, Palau), Gilbert Islands, Hawaii (Hawaii, Hilo, Kauai, Maui, Molokai, Oahu), Mariana Islands (Guam, Saipan), Marshall Islands, ?New Caledonia, Papua New Guinea [**new distribution**], Wake Island. Oriental: Japan (Ryukyus), Sri Lanka, Malaysia (Sarawak).

Remarks. A rather common, Indopacific species characterized by having uniformly yellowish body and male terminalia with anterior surstylus of peculiar and unmistakable shape (Sasakawa, 1995, fig. 6).

An updated checklist of the world species of *Dasyrhicnoessa* Hendel, 1934

Dasyrhicnoessa spp	distribution
aquila Munari, 2002	Australasian/Oceanian
atripes n.sp.	Australasian/Oceanian
bicolor Munari, 2002	Australasian/Oceanian
boninensis Sasakawa, 1995	Australasian/Oceanian
ciliata n.sp.	Australasian/Oceanian
clandestina Munari, 2002	Australasian/Oceanian
ferruginea (Lamb, 1914)	Afrotropical, South Indian Ocean Islands, Oriental, Australasian/Oceanian
fulva (Hendel, 1913)	Oriental
fulvescens Malloch, 1935	Australasian/Oceanian
humilis n.sp.	Australasian/Oceanian
insularis (Aldrich, 1931)	Nearctic, Neotropical, Afrotropical, Australasian/ Oceanian
longisetosa n.sp.	Australasian/Oceanian
mathisi Munari, 2002	South Pacific Islands
macalpinei n.sp.	Australasian/Oceanian
ostentatrix n.sp.	Australasian/Oceanian
pallida n.sp.	Australasian/Oceanian
platypes Sasakawa, 1986[a]	Oriental
priapus n.sp.	Australasian/Oceanian
serratula Malloch, 1935[b], sp.inq.	Australasian/Oceanian
sexseriata (Hendel, 1913)	Oriental, Australasian/ Oceanian
tripunctata Sasakawa, 1974	Oriental, Australasian/ Oceanian
vockerothi Hardy&Delfinado, 1980	Afrotropical, Oriental, Australasian/ Oceanian
yoshiyasui Sasakawa, 1986	Oriental

[a] *platypes* needs revision, its generic status being questionable.
[b] *serratula* of uncertain specific status.

Pseudorhicnoessa spinipes Malloch, 1914

Mathis & Munari, 1996: 13; Munari, 2002: 549–550.

Material examined. **Australia, Northern Territory**: Smith Point, Cobourg Pen., 5.iii.1996, D.K. McAlpine, 18♂♂ 7♀♀. **Australia, Queensland**: Kurrimine Beach, 43 km South of Innisfail, 23.i.1991, D.K. McAlpine & B. Day, 1♀; Lloyd Bay, 3 mi N of Claudie River mouth, on beach, 25.xii.1971, D.K. McAlpine and G.A. Holloway, 13♂♂ 15♀♀; Lloyd Bay, Lockhart River, MV lamp, 24.x.1974, G. and A. Daniels, 2♂♂ 4♀♀; Restoration Beach, near Portland Roads, 13.x.1974, G. Daniels, 4♂♂ 1♀; [as *P. tibiseta* (Mall.)] Townsville [type locality of the junior synonym *Tethina tibiseta* Malloch], [without date], F.H. Taylor, (SPHTM Coll.), 2♂♂ 2♀♀; [as *P. tibiseta* (Mall.)] *ibidem*, at light, 1♀. **Papua New Guinea**, Oro Bay, Northern Distr., 9.xii.1972, G.A. Holloway, 3♀♀; Port Moresby, Ela Beach, 6.x.1963, D.K. McAlpine, 10♂♂ 18♀♀; *ibidem*, 10.i.1964, 1♀.[AM]

Distribution. Australasian/Oceanian: Australia (NT [**new distribution**], QLD), Caroline Islands (Palau, Tobi, Yap), Mariana Islands (Guam, Saipan), Marshall Islands (Alu, Likiep, Majuro), Papua New Guinea [**new distribution**]. Oriental: Malaysia (Sabah, Sarawak, Singapore), Philippines, Japan (Ryukyus), Taiwan, Vietnam.

Sigaloethina n.gen.

Type species. *Sigaloethina phaia* n.sp. (Fig. 23).

Diagnosis. Dark flies having fairly to noticeably glossy cuticle; head higher than long; face depressed and partially membranous; lower face, above vibrissal angle, without tubercle (like *Dasyrhicnoessa*); cephalic chaetotaxy typical of subfamily (though with setulae of frons and vittae a little impoverished in numbers); frons without discernible shining patch on both sides of ocellar triangle; arista of postpedicel bearing spaced, long hairs; eye densely micropubescent, very large, its longest diameter over 8× as long as genal height. Thorax entirely dark brown, glossy, slightly convex dorsally, with chaetotaxy typical of subfamily; disc of scutellum bare; thoracic cuticle covered with more or less faint grey microtomentum. Legs evenly setulose except for foreleg having coxa and femur with long setae; ctenidium of fore femur vestigial or even absent; mid femur of male with row of posteroventral, spine-like setae on entire length of femur; all legs with femora dark brown, remaining parts yellow to yellowish brown. Wing like those in *Dasyrhicnoessa* species, that is with vein R_{2+3} slightly bisinuate; halter yellowish. Abdomen shining, black, with narrow, apicomarginal, pale brownish stripe on each tergite; tergites bearing several black setae and setulae. Male terminalia with lobe-shaped anterior surstylus (Fig. 24) noticeably larger than posterior surstylus, latter straight and relatively narrow; anterior surstylus bearing characteristic triangular patch of microtrichia on outer surface; both surstyli bearing several tubercles on inner sides (Fig. 25); cerci small; distiphallus (Fig. 26) fairly complex, bearing membranous lobe medially; postabdomen of female with two spherical, smooth spermathecae.

Remarks. *Sigaloethina* is closely related to *Dasyrhicnoessa* differing from it particularly in having the body cuticle noticeably glossy, the frons lacking a discernible shining patch on both sides of the ocellar triangle, the setal vestiture of the frons slightly, even though distinctly, sparce, and for the peculiar morphology of the male terminalia. On the basis of the present knowledge, *Sigaloethina* might be regarded as the sister group of *Dasyrhicnoessa*.

Etymology. The generic epithet derives from the fusion of the ancient Greek word *sigaloeis* meaning glossy or shiny, with the generic name *Tethina*, and refers to the body of these flies having glossy cuticle. Gender feminine.

Sigaloethina phaia n.sp.

Figs. 23–26

Type material. HOLOTYPE ♂ **Australia, New South Wales** "Mangroves / Careel Bay, / Avalon, NSW. / 3 Feb. 1973 / D.K. McAlpine // HOLOTYPUS / *Sigaloethina phaia* / gen. n., sp. n., ♂ / L. Munari des." AM K186743. The specimen is in excellent condition, and is double mounted (glued on the tip of a triangular card label); abdomen dissected and stored in glycerol in a small plastic tube, and pinned below the specimen. PARATYPES **Australia, New South Wales**: same data as holotype, 3♂♂ 11♀♀; "Careel Bay / N. South Wales / 27 Oct. 1962 // Mangroves / D.K. McAlpine", 1♂; *ibidem*, "14 March 1963", 1♀; "Careel Bay, / Avalon, NSW. / 15 Dec. 1964 / D.K. McAlpine // Mangroves", 1♂; *ibidem*, "26 Dec. 1964", 1♂; "North Creek, near / Ballina, NSW. / 1 March 1965 / McAlpine & Lossin", 1♀; "Mangroves, Nth / Cronulla, NSW. / 21 Jan. 1962 / D.K. McAlpine", 1♂; "NSW: Towra Pt., / Botany Bay; 29– / iii–1986; Bickel / mangroves", 1♂. **Australia, Northern Territory**: "NT: Buffalo Ck, / Darwin; 2–5 Mar. / 1996; D.K. McAlpine, / G.R. Brown", 1♂ 1♀. The holotype and most of the paratypes are deposited in AM, some paratypes are preserved in MCV.

Description. *Size*. Body length 2.1 mm (1.6–2.3), wing length 2.1 mm (1.5–2.3), wing width 0.8 mm (0.5–0.8). *Habitus* (Fig. 23). Dark brown species having glossy cuticle, generally covered with thin, greyish microtomentum. Wings yellowish grey. *Head*. Dark brown, except for anterior surface of frons, antenna, face, parafacial, and gena being yellow; frons without discernible golden patch on both sides

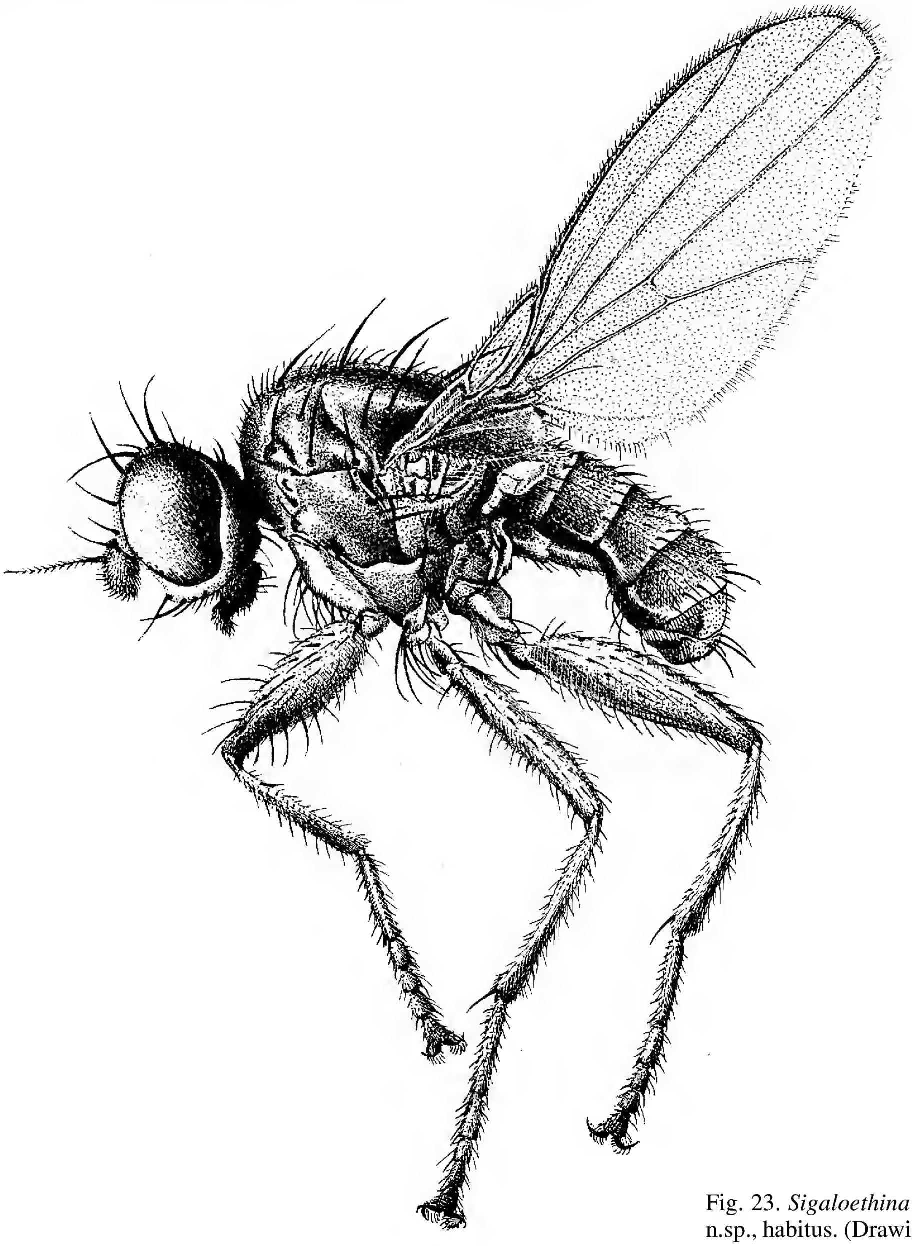


Fig. 23. *Sigaloethina phaia* n.gen. and n.sp., habitus. (Drawing by G. D'Este).

of ocellar triangle, or, if weakly present, absolutely not contrasting with rest of glossy, dark surface; paravertical setae thin, strongly inclinate; inner vertical seta inwardly curved, strong, about as long as lateroclinate outer vertical seta; postocular setae relatively long and strong, arranged in single row; upper postocular seta long, inclinate towards inner vertical seta; ocellar triangle bearing pair of thin pseudopostocellar setae in addition to pair of strong ocellars; 3 strong orbital setae, mid one distinctly lateroclinate, anterior and posterior setae more weakly lateroclinate to posteriorly directed; orbital vitta, apart from strong orbitals, almost entirely bare, at most with very few, thin setulae; 2 pairs of frontal setae, posterior pair with short, thin setae (some paratypes bear 1 to 3 pairs of such setae), anterior pair (in most paratypes equivalent to mid pair) with setae cruciate at apex; antenna with pedicel bearing very long dorsal seta, and postpedicel with arista bearing several long hairs; eye densely micropubescent, large, subrectangular, its longest diameter 8.2× as long as genal height; 7 black peristomal setae, four anteriors, including vibrissa, distinctly spaced, strong and long; shining knob above vibrissal angle absent (like *Dasyrhicnoessa*); mouth parts yellowish, with labellum small and stumpy, and palpus long and slender, bearing few black setulae. *Thorax*. Entirely dark brown, noticeably glossy, with setal vestiture black, mostly covered with light grey microtomentum; 1+3 dorsocentral setae; 4 rows of acrostichal setulae on entire length of scutum; prescutellar acrostichals long and thin; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta very long and strong, anterior setae shorter and weaker; 1 long presutural seta; 2 notopleurals subequal in length; 1 supra-alar, below it 1 shorter seta; 2 postalars, external one very long; scutellum bare, except for usual 4 long marginal setae; both proepisternal and proepimeral setae present, latter seta distinctly thinner; anepisternum with scattered pubescence, bearing 2–3 long, posteriorly directed, posteromarginal setae, mid one distinctly longer and stronger, and 1 erect, thin seta at posterodorsal margin; katepisternum with scattered pubescence, bearing long, erect, posterodorsal seta; anepimeron, katatergite, and meron without setae and setulae. *Legs*. Evenly setulose, bearing short blackish setae and setulae, except for foreleg having coxa with long black setae, and femur with very long, markedly spaced, posterodorsal and posteroventral setae; fore femur having vestigial ctenidium, at most with 1–2 spine-like setae (among the paratypes there are specimens without evident ctenidial spinulae, only with few, spaced, thin setae; conversely, a few other specimens show 1–4 weak, spaced spinulae which could represent the rudiments of a true ctenidium); mid femur of male with row of robust, subequal in length, posteroventral, spine-like setae arranged on entire length of femur; all legs show yellow coxae, dark brown femora, yellowish brown to yellow tibiae, and yellow tarsi; fore and hind femurs of male slightly swollen. *Wing*. Veins brownish yellow, membrane yellowish grey; alula with fringe formed by erect, blackish setae; costal vein reaching end of M_1 (sometimes as faint segment), bearing microscopic setulae on both dorsal and ventral surfaces; R_{2+3} slightly bisinuate, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending before middle of cell *dm*; crossvein *dm-cu* distinctly shorter than one third of last section of CuA_1; halter yellowish. *Abdomen*. Shining, black, with narrow, apicomarginal, pale brownish stripe on each tergite; tergites bearing several black setae and setulae. *Male terminalia* (Figs. 24–26). Epandrium broad, bearing sparse setae on posterior surface, few of them long and strong, in particular on dorsal surface and on posteromarginal part of distal half; cercus of normal size, pubescent, covered with microscopic hairs and with long setae dorsally; anterior surstylus arising from lower part of epandrium, distinctly larger than posterior surstylus, vaguely subtriangular, with external angles broadly rounded, its transverse axis almost perpendicular to longitudinal axis of epandrium, bearing patch of close microtrichia forming triangular area on outer surface, and with numerous, stout tubercles on posterior inner side; posterior surstylus simple, elongated, broadly rounded apically, bearing several stout tubercles on inner side; aedeagal apodeme long, bisinuate proximally; ejaculatory apodeme with broad distal fan; phallus (Fig. 26) relatively short; distiphallus with basal half distinctly sclerotized, bearing many spine-like papillae, distal half bearing strongly diaphanous membranous lobe, and with unusual, partly sclerotized folding zone dividing phallus in two halves.

Female. Similar to male, except for very slight sexual dimorphism. *Female terminalia*. Cerci slender, narrow, bearing setulae dorsally and apically; spermathecae spherical, smooth.

Distribution. Australia (NSW, NT).

Remarks. The two specimens from Buffalo Creek (Northern Territory) are smaller than the other paratypes from New South Wales. However, the male terminalia are similar and I regard the specimens from both areas as conspecific.

Etymology. From the ancient Greek *phaios* meaning dusky or brown. The specific epithet refers to the dark brown colour of the new species.

Sigaloethina sp. near *phaia* n.sp.

Material examined. **Australia, Queensland**: Gladstone, mangroves, 19.xii.1961, D.K. McAlpine, 1♀ [AM].

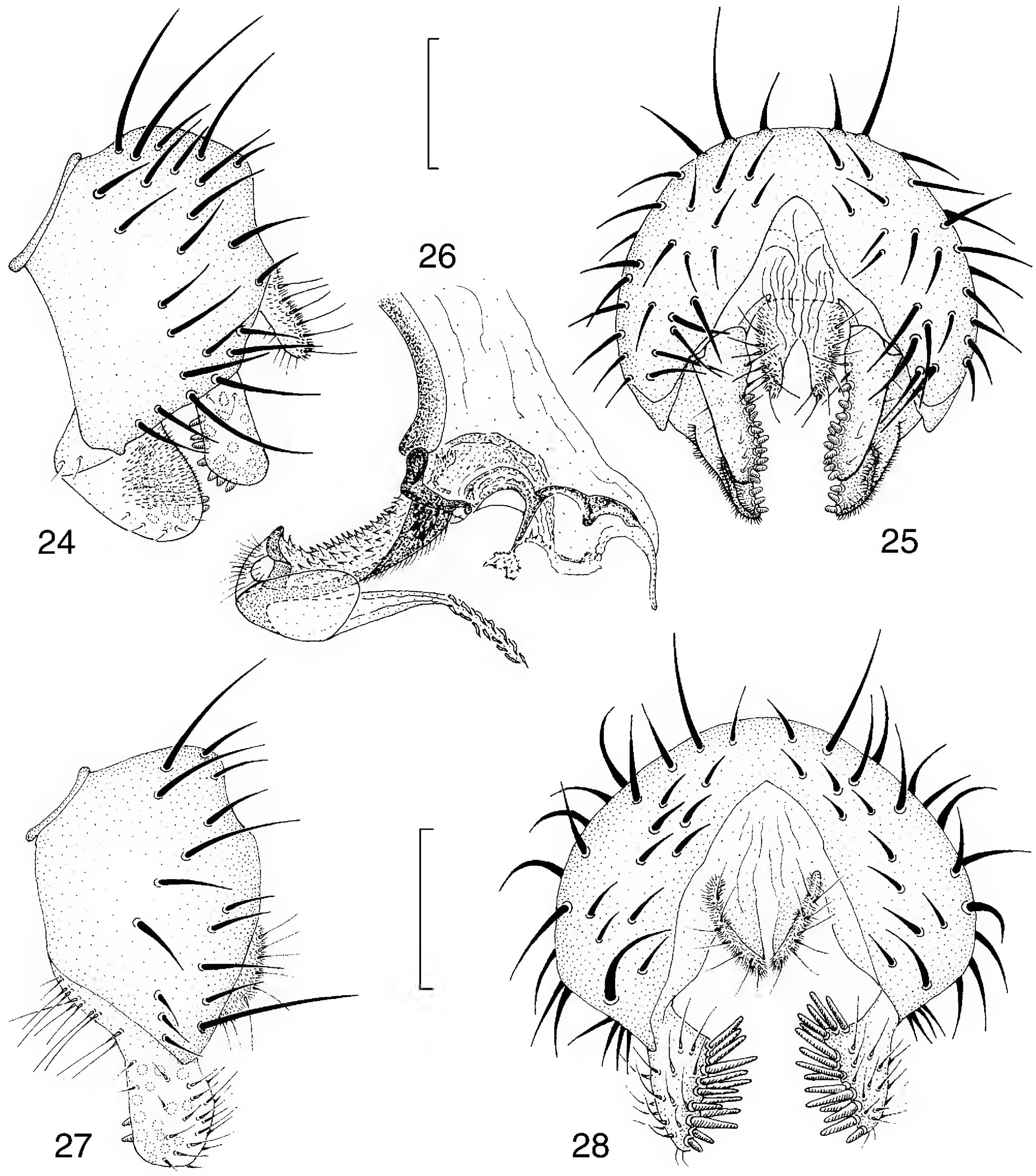
Remarks. The female specimen from Gladstone (QLD) shows a peculiar, dense microtomentum on the thorax and abdomen, resembling the characteristic pruinescence covering the peel of a plum. This specimen, labelled with the abbreviation “cf.”, might be an undescribed species.

Tethina nigriseta Malloch, 1924

Figs. 27–28

Mathis & Sasakawa, 1989: 668; Colless & D.K. McAlpine, 1991: 779; Mathis & Munari, 1996: 17.

Material examined. **Australia, New South Wales**: Booti-Booti Nat. Park, The Ruins, Forster District, shoreline rocks, 9.x.2000, D.K. McAlpine, 4♂♂ 1♀; Broken Head, near Byron Bay, shoreline rocks, 7–8.xi.2000, D.K.M., 3♂♂ 1♀; Bulli, adults emerged from kelp, 11.iii.1991, D.K.M., 2♂♂ 2♀♀; Bundagen, via Repton, 15.i.1971, D.K.M. & A. Hughes, 2♂♂ 19♀♀; Bundeena, near Sydney, on seashore rocks, 10.xii.1966, D.K.M., 1♂ 1♀; Careel Bay, 15.xii.1957, D.J.J. Lee, (SPHTM Coll.), 1♂; *ibidem*, 28.xii.1957, D.J.J. Lee, (SPHTM Coll.), 1♀; Collaroy, 20.i.1924, [no collector], (SPHTM Coll.), 1♀; Dee Why, near Sydney, sand hills, 31.iii.1962, D.K.M., 1♀; *ibidem*, sand dunes, 4.xi.1971, D.K.M. & G.A. Holloway, 30♂♂ 7♀♀; Iluka rain forest, Clarence River, MV lamp, 22.ii.1965, D.K.M., 1♀; *ibidem*, MV lamp, 24–25.xi.1970, D.K.M., 1♂ 2♀♀; Kurnell, on beach, 23.ii.1957,



Figs. 24–28. Terminalia of male. *Sigaloethina phaia* n.gen. and n.sp.: (24) lateral view, (25) posterior view, (26) phallus. *Tethina nigriseta* Malloch, 1924: (27) lateral view, (28) posterior view. Scale bars: 0.1 mm.

D.K.M., [D.K.M. det.], 3♂♂ 1♀; *ibidem*, 1.iii.1962, D.K.M., 12♂♂ 9♀♀; Little Beach, near Terrigal, on beach, 29.i.1988, D.K.M. & B.J. Day, 23♂♂ 31♀♀; Maitland Bay, near Terrigal, on beach, 29.i.1988, D.K.M. & B.J. Day, 40♂♂ 33♀♀; McMasters Beach, near Terrigal, on kelp, 25.xi.1987, D.K.M., R. Blanche, and B.J. Day, 1♀; *ibidem*, 29.i.1988, D.K.M. & B.J. Day, 6♀♀; North Beach, Bellinger River, sand dunes, 15.i.1971, D.K.M., 35♂♂ 35♀♀; Putty Beach, near Terrigal, 25.xi.1987, D.K.M., R. Blanche, and B. Day, 2♂♂ 2♀♀; Red Rock, near Woolgoolga, dunes, 9.xi.2000, D.K.M., 1♀; Seal Rocks (headland), shoreline rocks, 9–10.x.2000, D.K.M., 6♂♂ 8♀♀; Sydney, Narrabeen, 21.i.1924, Health Dept., (SPHTM Coll.), [J.R. Malloch det.], 1♂; Sydney, Long Reef, on intertidal rocks, 28.i.1964, D.K.M., 2♀♀; *ibidem*, on beach, 28.i.1964, D.K.M., 1♂; *ibidem*, on stranded kelp, 30.iii.1964, D.K.M., 4♂♂ 5♀♀; *ibidem*, on kelp, 26.iv.1984, D.K.M. & M. Dingley, 16♂♂ 40♀♀; Turimetta Beach, near Sydney, 2.v.1981, B.J. Day, 4♂♂ 1♀; Twofold Bay, Nullica Beach, stranded seaweed, 13.v.1988, D.K.M. & B.J. Day, 11♂♂ 7♀♀; Valla Beach, near Urunga, 23.ix.1981, D.K.M. & B.J. Day, 8♂♂ 3♀♀; Wairo Beach, near Durras, 11.iv.1986, D.K.M., 2♂♂ 1♀; Woody Head, near Iluka, 29.xii.1978, B.J. Day, 4♂♂ 8♀♀; Woolgoolga, shoreline rocks, 7.xi.2000, D.K.M., 1♂. **Australia, Victoria**: Mallacoota, Bastion Point, stranded seaweed, 13–14.v.1988, D.K.M. & B.J. Day, 1♂ 2♀♀; Walkerville, near Waratah Bay, on stranded seaweed, 6–7.iv.1986, D.K.M., 2♂♂ 1♀.

Distribution. Australia (NSW, QLD, VIC [**new distribution**]).

Remarks. This species is probably the most common tethinid fly inhabiting the shores of NSW and VIC.

Tethina pallidiseta Malloch, 1935

Mathis & Sasakawa, 1989: 668; Mathis & Munari, 1996: 17–18; Munari, 2000: 247.

Material examined. **Australia, New South Wales**: Careel Bay, 18.i.1958, D.J. Lee, (SPHTM Coll.), 2♂♂; Dee Why, near Sydney, 28.i.1957, W.W. Wirth, 1♂; *ibidem*, lagoon and sand hills, 31.iii.1962, D.K. McAlpine, 5♂♂ 8♀♀; *ibidem*, sand dunes, 4.xi.1971, D.K. McAlpine & G.A. Holloway, 4♂♂ 6♀♀; Iluka rain forest, Clarence River, MV lamp, 22.ii.1965, D.K. McAlpine, 1♀; *ibidem*, MV lamp, 24.xi.1970, D.K. McAlpine, 1♀; Kurnell, on beach, 23.ii.1957, D.K. McAlpine, 1♂; Long Reef, on beach, 28.i.1964, D.K. McAlpine, 2♂♂ 1♀; *ibidem*, on stranded kelp, 30.iii.1964, D.K. McAlpine, 1♀; Merimbula, Ocean Beach, 12.ii.1963, D.K. McAlpine, 1♀; North Beach, Bellinger River, 16.xi.1964, D.K. McAlpine, 2♀♀; *ibidem*, on beach, river side, 21.ii.1965, D.K. McAlpine, 1♀; *ibidem*, sand dunes, 15.i.1971, D.K. McAlpine, 3♂♂ 5♀♀; North Cronulla, sand dunes near sea, 3.iv.1962, D.K. McAlpine, 18♂♂ 5♀♀; Red Rock, near Woolgoolga, dunes, 9.xi.2000, D.K. McAlpine, 8♂♂ 9♀♀; Turimetta Beach, near Sydney, 2.v.1981, B.J. Day, 2♂♂ 1♀. **Australia, Lord Howe Island**, Old settlement Beach, 20.ii.1971, D.K. McAlpine, 18♂♂ 7♀♀; *ibidem*, Blinky Beach, 25.ii.1971, D.K. McAlpine, 1♂ 4♀♀. **Australia, Tasmania**: Bruny I., The Neck, 8.xii.1987, D.K. McAlpine, 2♀♀; Spring Beach, near Orford, 6–7.xii.1987, D.K. McAlpine, 2♀♀. **Australia, Victoria**: Venus Bay via Lower Tarwin, 8–9.iv.1986, D.K. McAlpine, 1♂ 3♀♀.

Distribution. Australia (NSW, TAS [**new distribution**], VIC [**new distribution**], WA) (see Munari [2000] for WA record).

Remarks. This species is very easily recognizable by its white setae and setulae.

Thitena n.gen.

Type species. *Thitena cadaverina* n.sp. (Fig. 29).

Diagnosis. Robust, yellowish brown flies with legs bearing strong setae and long and thick villosity which is particularly developed in male; head roundish; face depressed, bearing shining, foldlike tubercle above vibrissal angle; cephalic chaetotaxy typical of subfamily; frons without discernible golden patch on both sides of ocellar triangle, only with slight infuscation; arista microscopically pubescent; eye roundish, with few, sparse interfacetal setulae; longest diameter of eye over 3.5× as long as genal height. Thorax very slightly flattened dorsally, with chaetotaxy typical of subfamily; disc of scutellum pubescent (Fig. 30); all thoracic setae distinctly thinner than those in all other Tethininae. Legs very robust, strongly villose, particularly forelegs in male (an apomorphic character state with respect to the ground plan of the Tethinidae); tarsi of male stumpy, with tarsomeres noticeably short (in particular basitarsomeres), setulose, and flattened; true ctenidium absent; tibiae with rows of strong setae. Wing typical of subfamily; halter pale yellow. Abdomen rather robust, with tergites and sternites well sclerotized; male terminalia (Figs. 31–32) with very

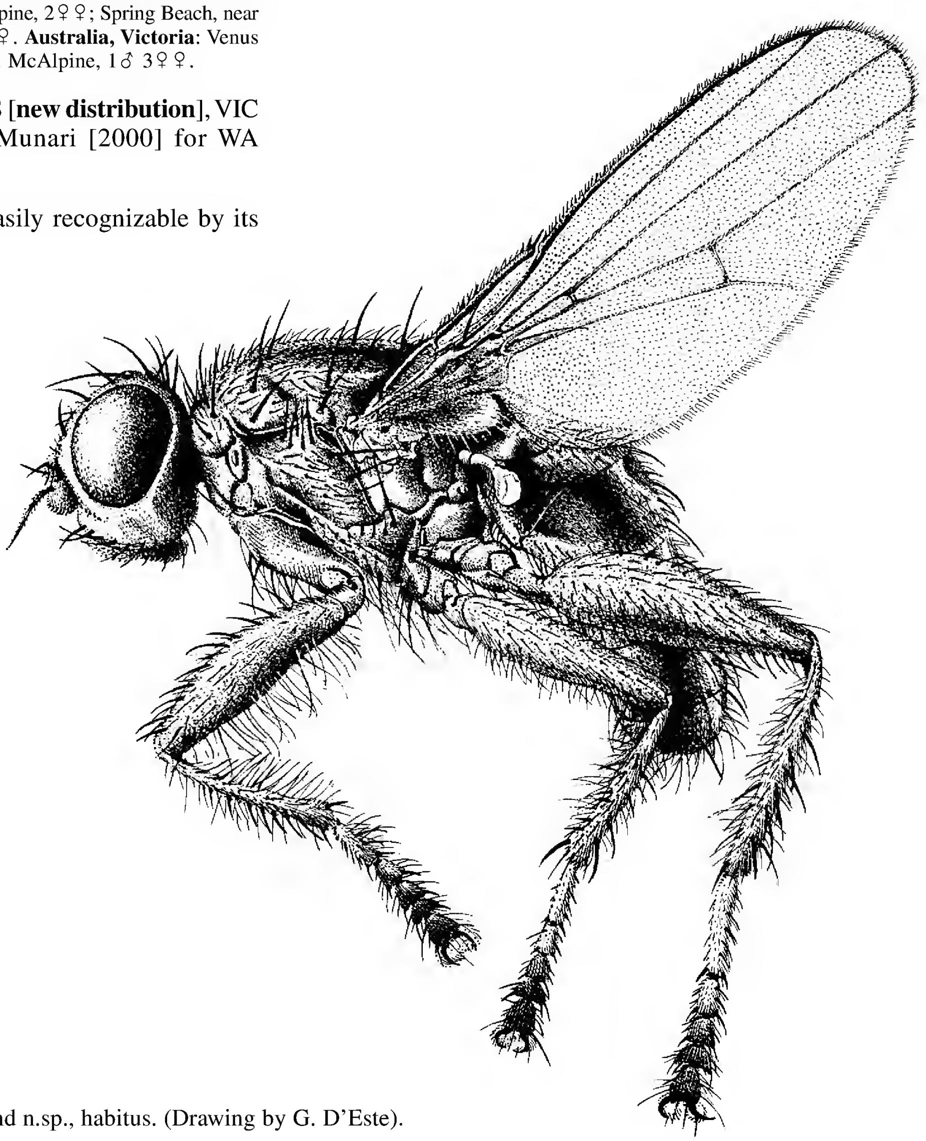


Fig. 29. *Thitena cadaverina* n.gen. and n.sp., habitus. (Drawing by G. D'Este).

long and slender anterior surstylus, and large posterior surstylus externally covered with dense microtrichia; both surstyli subequal in length and reciprocally parallel. Spermathecae of female spherical, smooth.

Remarks. For some morphological and chaetotactic traits as well as for the general habitus, the new genus would seem to be related to *Pseudorhicnoessa*, differing from it particularly for the following characters besides those given in the key: larger size; body and legs distinctly more robust and setulose; frons with numerous additional setulae; thoracic setae distinctly thinner; true ctenidium of fore femur absent; fore tibia with row of strong setae; mid and hind tibiae with different chaetotactic pattern; tarsi of male stumpy, with tarsomeres noticeably short (in particular basitarsomeres), setulose, and flattened; crossvein *dm-cu* longer, about as long as half of last section of CuA_1; abdomen with sternites well sclerotized; male terminalia with anterior and posterior surstyli subequal in length and reciprocally parallel.

Etymology. The generic epithet derives from an anagram of the generic name *Tethina*. Gender feminine.

Thitena cadaverina n.sp.

Figs. 29–32

Type material. HOLOTYPE ♂ **Australia, Western Australia** "Barrow Island / W. Australia / 12.ii.1977 H. H. 75 / H. Heatwole / W.H. Butler // On dead turnstone / 12 Feb. 1977 / Beach / Barrow Is. W.A. / H. H. 75. // HOLOTYPUS / *Thitena cadaverina* / gen. n., sp. n. ♂ / L. Munari des." AM K186744. The specimen is in fairly good condition (many setae missing, posterior edge of both the wings a little damaged), and is double mounted (glued on the tip of a triangular card label); abdomen, including terminalia, *in situ*. PARATYPES **Australia, Western Australia**: same data as holotype, 4♂♂ 7♀♀. The holotype and most of the paratypes are deposited in AM, a couple of paratypes is preserved in MCV.

Description. *Size*. Body length 4.1 mm (3.3–4.1), wing length 2.7 mm (2.2–2.7), wing width 1.0 mm (0.8–1.0). *Habitus* (Fig. 29). Robust, yellowish brown species with legs bearing strong setae and long and thick villosity. Wings brownish yellow. *Head*. Frons brownish yellow to brown, with very narrow, whitish orbital vittae; ocellar triangle and postcranial surface covered with dark grey microtomentum; antenna yellow, distinctly infuscated; face, parafacial, and gena pale yellowish, latter homogeneously microtomentose; frons without golden patch lateral to ocellar triangle, only with slight infuscation; paravertical setae strongly developed, cruciate at apex; inner vertical seta inclinate, strong, about as long as lateroclinate outer vertical seta; postocular and postgenal setae arranged in several irregular rows; 2 upper postocular setae inclinate towards paraverticals, external seta distinctly longer; ocellar triangle bearing pair of well-developed pseudopostocellar setae, distinctly longer than half of strong ocellars; a few very short setulae between ocellars and pseudopostocellars, and behind latter setae; 3 strong, lateroclinate orbital setae; several additional setulae between orbitals and frontals, distinctly more numerous between two anterior orbitals and anterior pairs of frontal setae; 3–4 pairs of strong, frontal setae intercalated with 3 pairs of shorter and weaker setae, all setae and setulae inclinate; antenna with postpedicel bearing microscopically pubescent arista; eye roundish, with strongly impoverished micropubescence formed by very few, sparse interfacetal setulae; longest diameter of eye 2.8–3.3× as long as genal height; 7 strong peristomal setae (including vibrissa) decreasing in length posteriad; very narrow, glossy stripe along peristomal edge, between this one and peristomal setae, ending above vibrissal angle to form foldlike, shining facial tubercle; face depressed, without median carina; mouth parts yellow, with labellum shorter than length of buccal cavity, and palpus long, slender, slightly clavate, bearing scattered, golden brown setulae. *Thorax*. Brownish, covered with dark grey microtomentum; postpronotal lobe yellowish, faintly shining, distinctly contrasting with rest of brown thoracic surface; setae of mesonotum brownish to black, noticeably thinner than those in all other Tethininae species; 1+3 dorsocentral setae; 8–9 rows of acrostichal setulae on anterior half of scutum, otherwise arranged in 6 rows; prescutellar acrostichals long; postpronotal lobe bearing 3 setae, each with different inclination, posterior seta very long, anterior setae shorter, remaining surface with numerous strong setulae; 1 presutural seta; 2 notopleurals subequal in length; 1 supra-alar, below it 1 shorter seta; 2 postalars, external one slightly, even though distinctly, longer; scutellum with 4 long marginal setae and many additional setulae on discal surface (Fig. 30); proepisternal and proepimeral setae subequal in length and strength; anepisternum with pubescence almost fully covering entire surface, bearing 3 long, posteriorly directed, posteromarginal setae, mid one long and strong, and 1–2 erect, thin setae at posterodorsal margin; katepisternum very poorly pubescent on mid and upper parts, but with dense and very long brown villosity on lower surface, bearing long, erect seta on posterodorsal margin; anepimeron, katatergite, and meron without setae and setulae. *Legs*. Ventral and posteroventral sides of all legs, in particular of forelegs, strongly shaggy in male and with rows of long and robust setae present in both sexes; foreleg having yellow coxa bearing several, long, black setae; ventral and posteroventral surfaces of both fore femur and tibia of male covered with thick, very long and rather ruffled, golden villosity; fore tibia with row of posterodorsal black setae; fore femur bearing few setae dorsally and row of several, long, posteroventral setae; ctenidium absent, only short row of long, thin, golden setae in its place; mid leg

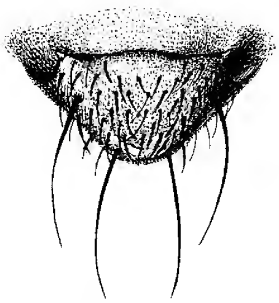
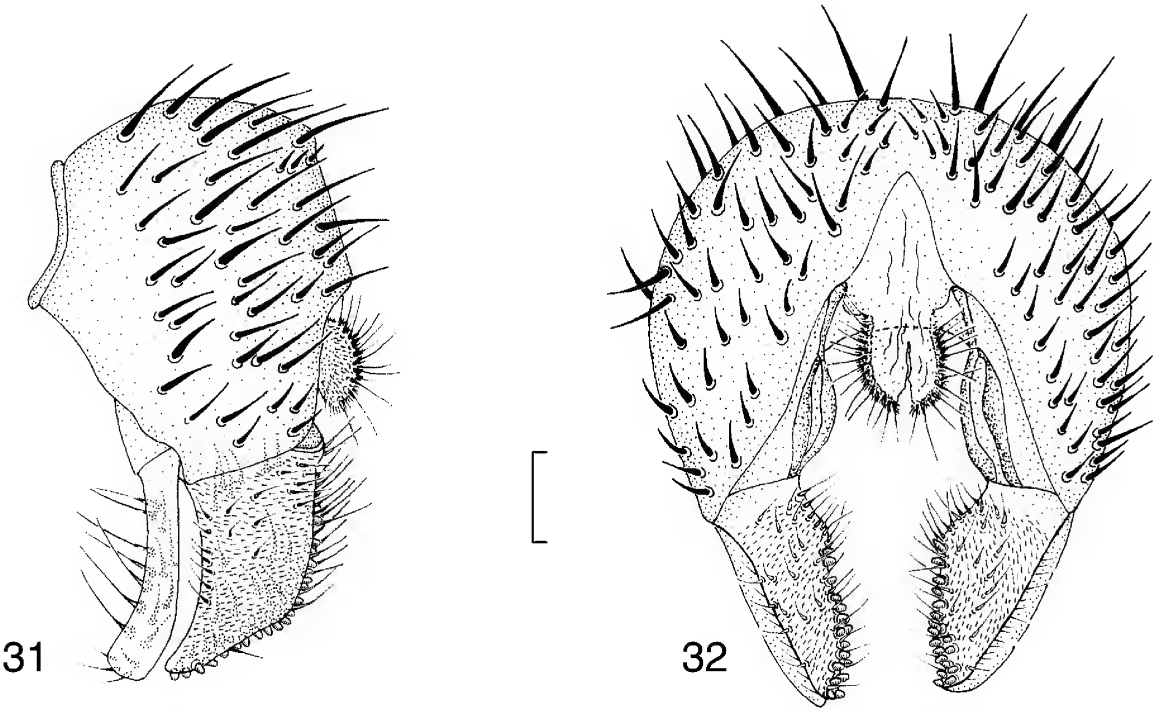


Fig. 30. *Thitena cadaverina* n.gen. and n.sp., scutellum dorsal view. (Drawing by G. D'Este).



Figs. 31–32. Terminalia of male. *Thitena cadaverina* n.gen. and n.sp.: (31) lateral view, (32) posterior view. Scale bar: 0.1 mm.

with more or less bristly femur, and with tibia bearing antero- and posterodorsal rows of strong and long setae on distal two thirds of its length; hind leg with femur distinctly swollen in male, and with tibia bearing anteroventral and antero- and posterodorsal rows of long and strong setae (in variable number) on distal two thirds of its length; tarsi of male stumpy, with tarsomeres noticeably short (in particular basitarsomeres), setulose, and flattened; all legs brownish, with last tarsomeres darker. *Wing*. Veins light brownish to yellowish, membrane brownish yellow; alula with fringe formed by several, erect, golden brown setae; costal vein reaching end of M_1, with apex of first section, just above subcostal break, bearing long and strong spine-like seta; dorsal and ventral surfaces of costal vein with hardly discernible, microscopic setulae; R_{2+3} almost straight to perceptibly bisinuate, slightly, even though distinctly, diverging from R_{4+5} distally; R_{4+5} and M_1 parallel; crossvein *r-m* ending before middle of cell *dm*; crossvein *dm-cu* about as long as half of last section of CuA_1; halter pale yellow. *Abdomen*. In male, with tergites and sternites well sclerotized, former rather broad, with narrow, yellowish, marginal stripes, and covered with several brownish to black setulae as well as with moderately long, golden brown, marginal setae which are longer on postabdominal segments; epandrium of male terminalia distinctly exposed. *Male terminalia* (Figs. 31–32). Entire surface of epandrium bearing numerous, short setae; cercus tiny, dorsally covered with microscopic hairs and with long setae; anterior surstylus very long and slender, about as long as posterior surstylus, narrow, slightly bent forwards, bearing very long, spaced, thin setae on inner side; posterior surstylus large, bent forwards, distinctly tapered and pointed apically (in lateral view), externally covered with dense microtrichia, bearing several thin setae and short, stout tubercles on inner side of posterior margin; aedeagal apodeme relatively short, sinuated medially; ejaculatory apodeme with distal fan poorly developed, having regular, subtriangular, unindented margin; distiphallus stumpy, short, ribbon-like, covered with dense micropubescence.

Female. All legs distinctly setulose, but without remarkable long villosity; for the rest, external morphology and chaetotaxy similar to male, except for slight sexual dimorphism; abdominal sternites well developed and distinctly sclerotized; 6th tergite and sternite large, latter with roundish margin; both tergites and sternites brown, bearing several marginal setae and setulae. *Female terminalia*. Cerci small, relatively short, setulose; spermathecae spherical, smooth.

Distribution. Australia (WA).

Remarks. More material of this interesting species is desirable as most of the type series is damaged. Many specimens have a collapsed thorax and many setae and setulae are missing.

Etymology. From the Latin *cadaverinus* meaning of dead body, corpse, carcass. The specific epithet refers to the substrate upon which the new species was collected: a dead Turnstone (a migratory shorebird of the genus *Arenaria*) possibly washed up on the beach.

A catalogue of the Tethininae of Australia and Papua New Guinea

Genus *Dasyrhicnoessa* Hendel

Dasyrhicnoessa Hendel, 1934: 38. Type species: *Rhicnoessa fulva* Hendel, by original designation.

***atripes* n.sp.** Distribution: Australia (NSW).

Dasyrhicnoessa atripes n.sp. (described in the present work) [New South Wales: Wategos, Cape Byron, beach; HT ♂, AM K186735; figures of ♂ terminalia].

***ciliata* n.sp.** Distribution: Australia (NT).

Dasyrhicnoessa ciliata n.sp. (described in the present work) [Northern Territory: Buffalo Ck, Darwin; HT ♂, AM K186736; figures of antenna and ♂ terminalia].

ferruginea (Lamb). Distribution, see text.

Rhicnoessa ferruginea Lamb, 1914: 367 [Seychelles: Mahé; LT ♂ (designated by Munari, 1988: 48), BMNH].

Tethina ferruginea.—Cogan, 1980: 693 [generic combination, Afrotropical catalog].

Dasyrhicnoessa ferruginea.—Munari, 1988: 48 [generic combination, lectotype designation].

fulvescens Malloch. Distribution, see text.

Dasyrhicnoessa fulvescens Malloch, 1935: 93 [Australia: Queensland, Townsville; HT ♀, AM].—Mathis & Sasakawa, 1989: 667 [Australasian/Oceanian catalog].—Munari, 2002: 550 [citation, world list].

***humilis* n.sp.** Distribution: Australia (NSW, QLD).

Dasyrhicnoessa humilis n.sp. (described in the present work) [New South Wales: Careel Bay, Avalon; HT ♂, AM K186737; figures of ♂ terminalia].

insularis (Aldrich). Distribution, see text.

Tethina insularis Aldrich, 1931: 395 [(USA) Wake Island; HT ♀, USNM (41629)].

Rhicnoessa insularis.—Hendel, 1934: 44 [key], 48 [generic combination, citation].

Dasyrhicnoessa insularis.—Hardy & Delfinado, 1980: 371–373 [generic combination, citation, figures of head, wing, ♂ and ♀ terminalia].—Munari & Evenhuis, 2000: 145–147 [revision, world distribution, citations].

Tethina lasiophthalma Malloch, 1933: 17 [Marquesas: Hivaoa, Tahauku; HT ♂, BPBM].

Dasyrhicnoessa lasiophthalma.—Sasakawa, 1974: 2 [generic combination].—Munari & Evenhuis, 2000: 145 [synonymy].

Dasyrhicnoessa ferruginea of authors, not Lamb, 1914 [misidentification].

Dasyrhicnoessa freidbergi Munari, 1994: 20 [Cameroon: Kribi (beach, Rt. N7); HT ♂, TAU].—Munari & Evenhuis, 2000: 145 [synonymy].

***longisetosa* n.sp.** Distribution: Australia (QLD), Papua New Guinea.

Dasyrhicnoessa longisetosa n.sp. (described in the present work) [Papua New Guinea: Port Moresby, mangroves; HT ♂, AM K186738; figures of ♂ terminalia].

***macalpinei* n.sp.** Distribution: Australia (NT).

Dasyrhicnoessa macalpinei n.sp. (described in the present work) [Northern Territory: Buffalo Ck, Darwin; HT ♂, AM K186739; figures of ♂ terminalia].

***ostentatrix* n.sp.** Distribution: Australia (NSW, VIC).

Dasyrhicnoessa ostentatrix n.sp. (described in the present work) [New South Wales: Careel Bay, Avalon, swept sea grass; HT ♂, AM K186740; figures of ♂ terminalia].

***pallida* n.sp.** Distribution: Australia (QLD).

Dasyrhicnoessa pallida n.sp. (described in the present work) [Queensland: Mackay, mangroves; HT ♂, AM K186741; figures of ♂ terminalia].

***priapus* n.sp.** Distribution: Australia (QLD).

Dasyrhicnoessa priapus n.sp. (described in the present work) [Queensland: Eurimbula, mangroves; HT ♂, AM K186742; figures of ♂ terminalia].

serratula Malloch [**sp. inq.**]. Distribution, see text.

Dasyrhicnoessa serratula Malloch, 1935: 94 [Australia: Queensland, Townsville; HT ♀, AM].—Mathis & Sasakawa, 1989: 667 [Australasian/Oceanian catalog].—Munari, 2002: 550 [citation, world list].

sexseriata (Hendel). Distribution, see text.

Rhicnoessa sexseriata Hendel, 1913: 110 [Taiwan: Anping; HT ♀, DEI].

Tethina sexseriata.—Steyskal & Sasakawa, 1977: 395 [generic combination, Oriental catalog].

Dasyrhicnoessa sexseriata.—Mathis & Munari, 1996: 12 [generic combination].

Dasyrhicnoessa asymbasia Sasakawa, 1995: 56 [Caroline Islands: Yap Islands, Rummang Island (at light); HT ♂, USNM; figures of ♂ terminalia].—Mathis & Munari, 1996: 12 [synonymy].

tripunctata Sasakawa. Distribution, see text.

Dasyrhicnoessa tripunctata Sasakawa, 1974: 5 [Philippines: Palawan, Tinabog (3 km NE); HT ♂, BPBM (10355)].

Dasyrhicnoessa phyllodes Sasakawa, 1995: 64 [Caroline Islands: Palau Islands, Babelthuap Island, Almongui (Ngaramlungui); HT ♂, USNM; figures of ♂ terminalia].—Munari, 1996: 10 [synonymy].

vockerothi Hardy & Delfinado. Distribution, see text.

Dasyrhicnoessa vockerothi Hardy & Delfinado, 1980: 373 [Hawaii: Kauai, Haena (collected on beach); HT ♂, BPBM].

Dasyrhicnoessa occidentalis Munari, 1986: 47 [Seychelles: Mahé, Mahé Beach (10 km N); HT ♂, MCV]; Munari, 1990: 53 [synonymy].

Genus *Plesiotethina* Munari

Plesiotethina Munari, 2000: 238. Type species: *Plesiotethina australis* Munari, by original designation.

australis Munari. Distribution: Australasian/Oceanian: Australia (WA).

Plesiotethina australis Munari, 2000: 240 [Australia: southwest Australia, south of Shoal Bay (6 km S Albany; salt meadow); HT ♂, ZSM; figures of head and ♂ terminalia].

Genus *Pseudorhicnoessa* Malloch

Pseudorhicnoessa Malloch, 1914: 306. Type species: *Pseudorhicnoessa spinipes* Malloch, by original designation.

Macrotethina Malloch, 1935: 91 (as a subgenus of *Tethina*). Type species: *Tethina (Macrotethina) tibiseta* Malloch, by original designation.

spinipes Malloch. Distribution, see text.

Pseudorhicnoessa spinipes Malloch, 1914: 307 [Taiwan: Takao; HT ♀, USNM].—Munari, 2002: 549, 550 [citation, Malaysia, Philippines, Australia (QLD), discussion].

Tethina (Macrotethina) tibiseta Malloch, 1935: 91 [Australia: Queensland, Townsville; HT ♂, AM].

Pseudorhicnoessa tibiseta.—Mathis & Sasakawa, 1989: 667 [generic combination, Australasian/Oceanian catalog].—Munari, 2002: 549 [synonymy].

Genus *Sigaloethina* n.gen.

***Sigaloethina* n.gen.** (described in the present work). Type species: *Sigaloethina phaia* n.sp.

***phaia* n.sp.** Distribution: Australia (NSW, NT).

Sigaloethina phaia n.sp. (described in the present work) [New South Wales: Careel Bay, Avalon, mangroves; HT ♂, AM K186743; figures of habitus and ♂ terminalia].

Genus *Tethina* Haliday

Tethina Haliday, in Curtis, 1837: 293 (as a subgenus of *Opomyza*; published in synonymy; first made available by use in Haliday, 1838: 188). Type species: *Opomyza (Tethina) illota* Haliday, 1838, by subsequent monotypy (Haliday, 1838: 188).

hirsuta Munari. Distribution: *Australasian/Oceanian*: Australia (WA).

Tethina hirsuta Munari, 2000: 244 [Australia: southwest Australia, Hopetoun (southern coast); HT ♂, ZSM; figures of head, legs, abdomen, ♂ terminalia, spermathecae].

nigriseta Malloch. Distribution, see text.

Tethina nigriseta Malloch, 1924: 337 [Australia: New South Wales, Woolgoolga; HT ♂, AM].—Mathis & Sasakawa, 1989: 668 [Australasian/Oceanian catalog].—Colless & D.K. McAlpine, 1991: 779 [figures of head and wing].

Rhicnoessa nigriseta.—Hendel, 1934: 43 [key], 47 [citation].

Tethina (Tethina) nigriseta.—Malloch, 1935: 92 [citation].

ochracea (Hendel). Distribution: *Afrotropical*: Cape Verde Islands, Senegal, Seychelles (Aldabra), South Africa. *Australasian /Oceanian*: Australia (WA). *Oriental*: Taiwan. *Nearctic*: Bermuda, USA. *Neotropical*: Chile, Mexico. *Palaearctic*: Algeria, Azores, Bulgaria, Canary Islands, Egypt, France, Greece, Israel, Italy, Madeira, Malta, Spain (including Balearic Islands), Tunisia, Turkey.

Rhicnoessa ochracea Hendel, 1913: 109 [Taiwan. Anping; LT ♂ (designated by Munari, 1991: 166), NMW].

Tethina ochracea.—Steyskal & Sasakawa, 1977: 395 [generic combination, Oriental catalog].—Munari, 2000: 247 [citation, Australia (SW)].

Rhicnoessa texana Malloch, 1913: 148 [USA. Texas. Nueces: Corpus Christi; HT ♀, USNM (15807)].

Tethina texana.—Sturtevant, 1923: 7 [generic combination].—Munari & Evenhuis, 2000: 147 [synonymy].

Tethina chilensis Malloch, 1934: 455 [Chile: Antofagasta, Antofagasta; HT ♂, USNM (allotype on same pin)].—Munari & Evenhuis, 2000: 147 [synonymy].

Tethina canzonerii Munari, 1981: 142 [Turkey: Karatàs; HT ♂, MCV]; Munari, 1991: 165 [synonymy].

pallidiseta Malloch. Distribution, see text.

Tethina (Tethina) pallidiseta Malloch, 1935: 92 [Australia: New South Wales, Collaroy; HT ♂, AM].—Mathis & Sasakawa, 1989: 668 [Australasian/Oceanian catalog].—Munari, 2000: 247 [citation, Australia (WA), figure of ♂ terminalia].

Genus *Thitena* n.gen.

***Thitena* n.gen.** (described in the present work). Type species: *Thitena cadaverina* n.sp.

***cadaverina* n.sp.** Distribution: Australia (WA).

Thitena cadaverina n.sp. (described in the present work) [Western Australia: Barrow Island, on dead Turnstone; HT ♂, AM K186744; figures of habitus, scutellum, and ♂ terminalia].

Conclusions

Even though restricted to the subfamily Tethininae, I hope that this study, together with an earlier paper on the beach flies from the southwestern coast of Australia (Munari, 2000), lays the foundations for further research. This study suggests that *Tethina* is much less diverse in species than *Dasyrhicnoessa. Tethina* species mainly inhabit maritime sandy beaches, that are, in some localities, subject to anthropogenic effects related to leisure and industry. Conversely, *Dasyrhicnoessa* species mainly occur in inhospitable environments such as mangrove forests around lagoons and inland bodies of water, or impenetrable littoral belts. These two particular littoral ecosystems have produced in the past, differing speciation rates within these two genera. It appears that the genus *Tethina* is poorly represented in Australia whereas the pan-tropical *Dasyrhicnoessa* has many species awaiting discovery. A similar situation exists with the better known Afrotropical fauna where the endemic *Afrotethina* is far more numerous than *Tethina.*

The data on the beach flies of Papua New Guinea are too scant to allow a fair assessment of its fauna. Possibly the Tethinidae of Papua New Guinea are more similar to the fauna of Malaysia and Melanesia.

With regard to Australia, our knowledge contains a huge gap as little is known about the Tethinidae of Northern Territory, Western Australia and South Australia. An indication of this may be the fact that two new genera and three new species from Western Australia, including *Thitena cadaverina* described here, have been found from scanty material, fruit of quite occasional dipterological collections.

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Appendix—Tethinidae from Pacific islands

In the material examined there were a few specimens from some Pacific Ocean islands; this material is cited below:

Dasyrhicnoessa clandestina Munari, 2002

(Munari, 2002: 543)

Material examined. **Fiji Islands**, Suva, xii.1929, K62562, H.R. Rabone, 1♂ [AM].

Distribution. Australasian/Oceanian: ?New Caledonia, Fiji.

Dasyrhicnoessa insularis (Aldrich, 1931)

(See citations in the main text)

Material examined. **Fiji Islands**, Suva, xii.1929, K62562, H.R. Rabone, 1♂ [AM].

Remarks. Five females captured in association with both the male specimens of this and the previous species (*D. clandestina)* have no consistent diagnostic character for separation, and are provisionally treated as "*Dasyrhicnoessa* cf. *clandestina/insularis*".

Dasyrhicnoessa cf. *insularis* (Aldrich, 1931)

Material examined. **French Polynesia, Society Is.,** Moorea, viii.1928, A. Tonnoir, 1♀ [AM]

Remarks. After examining this female specimen, merely named on label "*Dasyrhicnoessa uniformis*, Type" by Malloch but neither described nor published as a new species, I feel it should be regarded, tentatively, as *Dasyrhicnoessa insularis* (Aldrich).

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Systematics of Sphagnum Frogs of the Genus *Philoria* (Anura: Myobatrachidae) in Eastern Australia, With the Description of Two New Species

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ABSTRACT. Analyses of allozyme and mitochondrial nucleotide sequence variation in *Philoria* from northeastern NSW and southeastern Queensland revealed that there are more species than the three that are currently recognized. In addition to the three species presently recognized *P. kundagungan, P. loveridgei*, and *P. sphagnicolus*, another two species *P. pughi* n.sp. and *P. richmondensis* n.sp. were recognized under the evolutionary species concept. All species are allopatric. Each of the five species had two or more fixed genetic differences with all other species. Additionally, each species possessed two or more unique allozyme characters (apomorphies). Each species had strongly supported reciprocally monophyletic mitochondrial haplotypes in comparison with each of the other species. Multivariate morphometric analysis was able to distinguish *P. sphagnicolus* from the remaining four northern taxa but was unsuccessful in reliably distinguishing the two new species. Mating call analysis identified two distinct call groups: *P. sphagnicolus* and the remaining species, the latter showing little discrimination between species. The distribution of *Philoria* in NSW and Queensland shows a strong association with high rainfall rainforest at mid to high altitudes (above 600 m elevation). The habitat of all species is remarkably similar, all are found predominantly in the headwaters of rainforest streams or soaks on the forest floor. All species lay their eggs in nests in the ground, where the larvae remain throughout their entire development until they emerge post metamorphosis. It was confirmed that nests where the embryos were at an early stage of development were of two types: foaming egg masses, and nests containing a non-foaming jelly substance. All species are limited in their distribution. In particular *P. richmondensis* is in need of special conservation consideration, as it is known from only three localities within a very small range. A number of populations in southeastern Queensland and northern NSW await molecular analysis to be identified with certainty.

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The montane rainforest frogs of the genus *Philoria*, commonly known as "sphagnum frogs" are confined to the Great Dividing Range of eastern Australia (Barker *et al.*, 1995). *Philoria frosti* is the only member of the genus that is not a rainforest species, occurring above the snow line on the Mt Baw Baw plateau in Victoria (Malone, 1985), and it is not dealt with further in the present study. The remaining three members of the genus, *P. kundagungan* (Ingram & Corben, 1975), *P. loveridgei* (Parker, 1940) and *P. sphagnicolus* (Moore, 1958), are found in rainforests from the Mistake Mountains, near Warwick, Queensland, apparently to the Barrington Tops National Park, NSW in the south (Ingram & Corben, 1975; Wotherspoon, 1981). Other than brief habitat and ecological descriptions included in the original species descriptions, only *P. sphagnicolus* has had any aspects of its biology studied in detail (Anstis, 1981; de Bavay, 1993; Webb, 1989).

In Australia, 57 of an estimated 194 frog species have been reported in various stages of decline. This represents nearly a third of all Australian frogs (Vial & Saylor, 1993). The montane rainforest species of *Philoria* occur in similar rainforest habitats to several Australian frogs that have disappeared (Mahony, 1996). *Philoria kundagungan* and *P. sphagnicolus* are both found in close association with rainforest streams. Furthermore, populations of their nearest evolutionary relative, *P. frosti*, have recently significantly declined (Hollis, 1995). It is possible that gaining an understanding of the population genetics and ecology of these species of *Philoria* may shed some light on the broader question of the disappearance of eastern Australian frogs.

Philoria kundagungan, P. loveridgei and *P. sphagnicolus* are listed as "Vulnerable" under the New South Wales *Threatened Species Conservation Act, 1995*, and the first two are listed as "Rare" in the Queensland *Nature Conservation Act*, 1994. Two fauna surveys funded by NSW National Parks and Wildlife Service in 1989 in the Focal Peaks (Smith *et al.*, 1989b) and Mt Warning caldera (Smith *et al.*, 1989a) regions of northern NSW, both concluded that *Philoria* occurring in these areas were among "… the species most in need of monitoring and special consideration".

Wildlife managers currently consider the conservation of these species as a high priority (NSW NPWS, 1994). They are among the rarest vertebrates in eastern Australia. *Philoria kundagungan* for instance, is known from only eight localities, all within a very small range. All of the species are habitat specialists restricted to high mountains and throughout their ranges they have been subject to ongoing habitat fragmentation by humans. The need to increase our knowledge of all aspects of the biology of *Philoria* is now being highlighted as a result of legislative protection conferred upon frogs. Three species, *Philoria kundagungan, P. loveridgei* and *P. sphagnicolus*, are currently listed as "Vulnerable" in the New South Wales *Threatened Species Conservation Act, 1995*, and the first two are listed as "Rare" in the Queensland *Nature Conservation Act*, 1992. No species are listed as nationally endangered under the Commonwealth's *Environment Protection and Biodiversity Conservation Act, 1999*. A Fauna Impact Statement with regard to *P. sphagnicolus* in a proposed development area has been required already of a local government council on the NSW north coast by the NSW NPWS (Knowles & Mahony, 1993).

Specimens of *Philoria* collected recently during biological surveys conducted by the North East Forests Biodiversity Study, New South Wales National Parks and Wildlife Service (abbreviated NEFBS hereafter) have not readily conformed to previous taxonomic descriptions. Specimens collected from the Gibraltar Range, outside of the previously known ranges of *P. sphagnicolus, P. loveridgei* and *P. kundagungan* have been attributed by different workers to all three species (Australian Museum records, 1993; Queensland Museum records, 1993; NEFBS, unpublished). Different workers have also attributed specimens collected from Mt Warning NSW to either *P. sphagnicolus* or *P. loveridgei* (Australian Museum records, 1993; Queensland Museum records, 1993). The lack of precision in the systematic knowledge of the endangered montane rainforest species of *Philoria* is a severe handicap to efforts to conserve and appropriately manage them. An understanding of the taxonomy, conservation genetics and ecology of the species of *Philoria*, is therefore likely to be crucial to any future efforts to conserve them.

We use a combination of allozyme electrophoretic, mitochondrial nucleotide sequence and morphological analyses to establish a robust species-level systematic framework for *Philoria* in New South Wales and Queensland. We also assess the conservation status of each of the identified species and document the habitat characteristics of the species. The application of the techniques of allozyme electrophoresis and mitochondrial DNA sequencing to define species genetically, followed by morphometric analysis using the groupings so defined, has had significant success in resolving species boundaries within several Australasian vertebrate groups (e.g., Donnellan *et al.*, 1999; Mahony *et al.*, 2001).

Materials and methods

Allozyme electrophoresis. Frozen liver samples were available from 81 specimens of *Philoria* from 23 locations. (Fig. 1 and Appendix). Museum registration numbers and collection locality details are given in the Appendix. Samples from type locations were included where available. Allozyme electrophoresis of liver homogenates was conducted on cellulose acetate gels ("Cellogel", Chemetron) according to the methods of Richardson *et al.* (1986). The proteins and enzyme products of 34 presumed loci were scored. The proteins that were stained, abbreviations used (Murphy *et al.*, 1996), and their Enzyme Commission numbers (International Union of Biochemistry, 1984) are aspartate aminotransferase (AAT, E.C. 2.6.1.1), aconitate hydratase (ACOH, E.C. 4.2.1.3), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), aldehyde dehydrogenase (ALDH, E.C. 1.2.1.5), carbonate dehydratase (CA, E.C. 4.2.1.1), cytosol aminopeptidase (CAP, E.C. 3.4.11.1), enolase (ENO, E.C. 4.2.1.11), esterase (EST, E.C. 3.1.1.1), fructose-biphosphatase (FBP, E.C. 3.1.3.11), fumarate hydratase (FUMH, E.C. 4.2.1.2), glycerol-3-phosphate dehydrogenase (G3PDH, E.C. 1.1.1.8), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), glutamate dehydrogenase (GTDH, E.C. 1.4.1.3), L-iditol dehydrogenase (IDDH, E.C. 1.1.1.14), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), lactate dehydrogenase (LDH, E.C. 1.1.1.27), lactoyl-glutathione lyase (LGL, E.C. 4.4.1.5), malate dehydrogenase (MDH, E.C. 1.1.1.37), mannose-phosphate isomerase (MPI, E.C. 5.3.1.8), nucleoside triphosphate adenylate kinase (NTAK, E.C. 2.7.4.10), peptidases (PEP, E.C. 3.4.11 or 13.*), phosphoglycerate mutase (PGAM, E.C. 2.7.5.3), 6-phosphogluconate dehydrogenase (PGDH, E.C. 1.1.1.44), phosphoglycerate kinase (PGK, E.C. 2.7.2.3), phosphoglucomutase (PGM, E.C. 2.7.5.1), superoxide dismutase (SOD, E.C. 1.15.1.1), and triose phosphate isomerase (TPI, E.C. 5.3.1.1).

Alleles were identified by comparison with samples that were repeatedly included on each gel (internal controls) and through critical side-by-side comparisons (line-ups; see Richardson *et al.*, 1986). For analysis of the allozyme data, specimens of a single genetic type (i.e., a sample with all expected genotypes at variable loci under the assumption of Hardy-Weinberg equilibrium for a single interbreeding population) from a single locality were treated as an OTU (Operational Taxonomic Unit). Geographically proximate OTUs that consisted of a single genetic type were pooled. Cavalli-Sforza & Edwards (CSE) chord distances (Cavalli-Sforza & Edwards, 1967) were calculated with BIOSYS (Swofford & Selander, 1989). A phenogram was constructed from the genetic distances with the neighbour-joining algorithm (NJ—Saitou & Nei, 1987) in PHYLIP version 3.5c (Felsenstein, 1993). A maximum parsimony (MP) analysis was also performed using the heuristic search option of PAUP* 4.0d64 (Swofford, 1999). Loci were treated as characters, alleles as character states and multistate characters were treated as "uncertain" following the recommendation of Kornet & Turner (1999). Support for lineages was assessed with split decomposition using SplitsTree version 3.1 (Dress *et al.*, 1996; Huson, 1998)

Mitochondrial DNA analysis. See the Appendix for details of specimens examined. Total cellular DNA was extracted from frozen liver with the salting out procedure of Miller *et al.* (1988) and stored at -20°C. The same procedure was used to extract DNA from museum vouchers with the modification that the tissue, usually liver, was rinsed several times in TE buffer prior to proteinase K digestion to remove any alcohol. For polymerase chain reaction (PCR) amplifications, 50–100 ng of DNA was added to a 50 µl reaction mixture containing 4 mM MgCl$_2$, 1X reaction buffer, 0.8 mM dNTPs, 0.4 mM primers, 1 unit of Biotech *Tth* plus DNA polymerase and the remaining volume of dH$_2$O. The primers used for amplification of *ND4*, Limno2 [5'-TGA CTA CCA AAA GCT CAT GTA GAA GC-3'] and ND4 [5'-GRA ATG GNG RGA GGG YTT TTC G-3'], were designed by Schauble *et al.* (2000) and Arévalo *et al.* (1994) respectively. Amplifications, carried out on a Corbett FTS-320 Thermal Sequencer, comprised a single cycle of denaturation for 3 min at 94°C, annealing for 45 s at 55°C and extension for 1 min at 72°C, followed by 29 cycles of 94°C for 45 s, 55°C for 45 s and 72°C for 1 min, ending with a single extension step of 72°C for 6 min. PCR products were purified for sequencing using a Bresa-Clean DNA Purification Kit (Bresatec). Both strands were sequenced directly from each PCR product using the original PCR primers. Products were cycle-sequenced on a Corbett FTS-1 Thermal Sequencer using the Applied Biosystems PRISM Ready Reaction DyeDeoxy Terminator Cycle sequencing kit, following the manufacturer's instructions. The sequencing program comprised 25 cycles of 94°C for 30 s, 50°C for 15 s and 60°C for 4 min. Cycle-sequenced product was electrophoresed and viewed on an Applied Biosystems Model 373A Sequencing System.

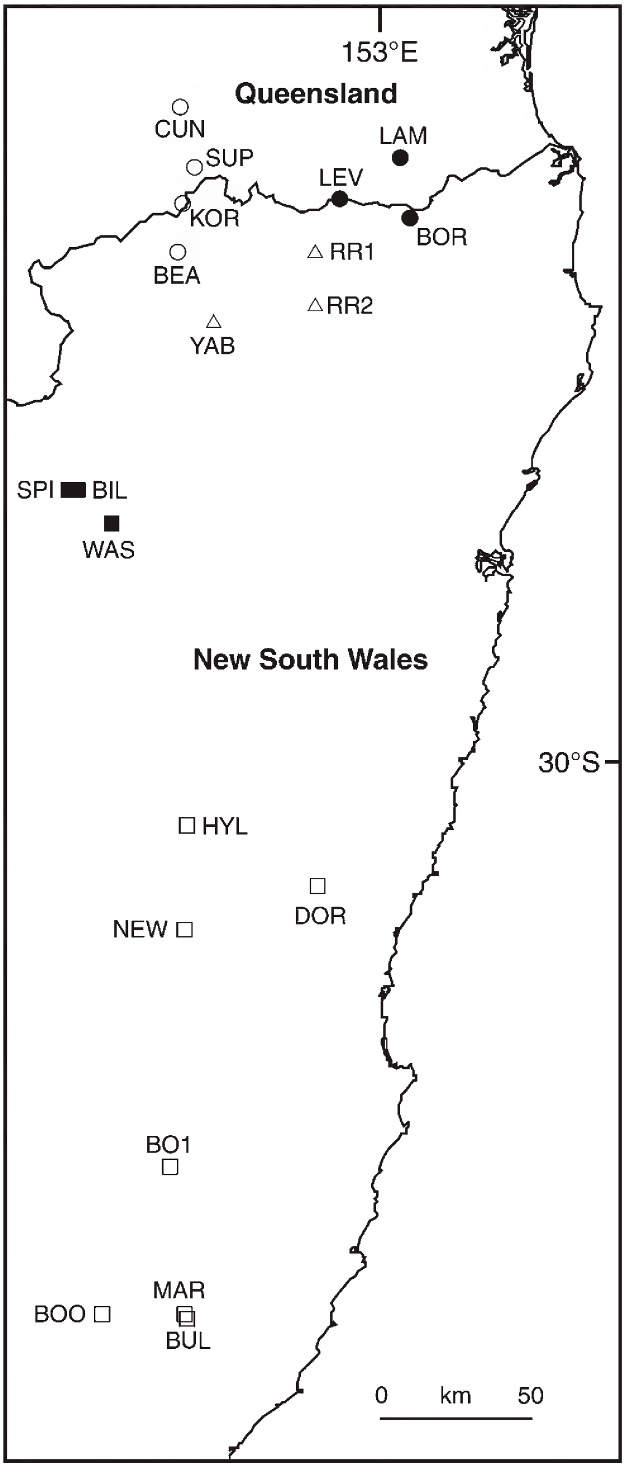

Fig. 1. Map of eastern Australia showing the collection localities for *Philoria*. Abbreviations refer to localities examined for genetic analyses, details of which are listed in the Appendix. Symbols: ○ *P. kundagungan*, ● *P. loveridgei*, ■ *P. pughi*, △ *P. richmondensis*, □ *P. sphagnicolus*.

A study of relationships within the family Myobatrachidae based on mitochondrial nucleotide sequence data (M. Cunningham, pers. comm.) shows that *P. frosti* is the sister lineage of the species of *Philoria* from northern New South Wales and southeastern Queensland. However, we were unable to amplify *ND4* from *P. frosti.* Instead, a range of limnodynastine genera, *Adelotus brevis, Crinia deserticola* *and Limnodynastes convexiusculus*, sequenced by Schauble *et al*. (2000), were used as outgroups. Sequences were aligned by eye as the alignment did not require the insertion of gaps. Evolutionary trees, constructed with the maximum parsimony (MP), and maximum likelihood (ML) criteria of optimality, were found with heuristic searches implemented in PAUP* 4.0b6 (Swofford, 1999). Modeltest version 3.0 (Posada & Crandell, 1998) was used to assess the most suitable model of nucleotide substitution from the data by hierarchal likelihood ratio tests. Specific model parameters for likelihood analyses were estimated from the data using PAUP* (e.g., base frequencies, transition/transversion ratios, I and Γ) by an iterative quartet puzzling method (Leys *et al*., 2000). The robustness of phylogenetic hypotheses was tested with bootstrapping.

A second set of PCR primers, M372 [5'-GCC GCC GCT CTT CTC TGT AT-3'] and M373 [5'-GGA AGA GAC TAG GCC GTG GG-3'], was designed to amplify a smaller 162bp product from selected museum vouchers. The product, which was sequenced directly, was designed to sample enough diagnostic sites to allow identification of individuals to species.

Morphological analysis. Adult specimens that were allozyme genotyped were included in the morphometric analysis as well as adult specimens held in the Australian and Queensland Museums and the holotypes of each of the described taxa (Appendix). The following characters were measured: snout-vent length (SVL); head width (HW) measured at the widest portion of the skull; head length (HL) measured between the angle of the maxilla and mandible, and the anterior tip of the jaw; tibia length (TL) measured with the knee and ankle joint fully flexed; eye width (E) with the specimen held horizontal; eye to naris distance (EN) from the anterior corner of the eye to the opening of the external naris (nostril) and inter-narial distance (IN) between the external nares. Measurements from formalin-fixed, alcohol-preserved specimens were made with vernier callipers to the nearest 0.5 mm or with an eyepiece graticule on a dissecting microscope. Sex was determined from observation of the presence of a nuptial pad in adults or examination of gonad morphology by dissection.

Colour pattern descriptions are based on live and freshly dead specimens.

Discriminant function analysis (DFA) was conducted with the program Statistica release 5.1, 1997 edition (StatSoft, 1997) to assess differentiation in body shape between the genetic groups. The DFA used the seven variables described above.

Male advertisement call analysis. Analyses were conducted of the male advertisement calls of *Philoria* to determine whether genetically defined groups have diverged in call characteristics. Sound recordings were made of the advertisement calls of male frogs in the field using a Sony WMD6 tape recorder and directional microphone. A minimum of five calls was analysed per male. Call attributes including call (=note) duration, call repetition rate, pulse repetition rate, pulses per call, and dominant frequency range were analysed from audio spectrograms, waveforms and frequency spectra using the sound analysis package Avisoft-SASLab Pro©, 2001.

Larval morphology. The development stage of eggs and larvae were determined under a dissecting microscope according to the criteria of Gosner (1960).

Results

Allozyme electrophoretic data. Table 1 gives the allozyme profiles of the 20 OTUs. For *P. sphagnicolus*, 34 loci were scored, whereas 32 loci were scored for the remaining OTUs of *Philoria*. These data were then converted into matrices of percentage of loci showing fixed allelic differences and CSE chord distances between OTUs.

A NJ phylogram constructed from CSE chord distances between OTUs is presented in Fig. 2A. The BO2 OTU was not included because it appears to be a possible F_1 hybrid (see below), and including a hybrid in an analysis that attempts to produce dichotomous branching trees invalidates an assumption of the algorithm. The OTUs fall into two major genetic clusters: a northern cluster comprising CUN, SUP, KOR, BEA, LAM, BOR, YAB, RR1, RR2, BIL, SPI and WAS and a southern cluster comprising *P. sphagnicolus*—HYL, NEW, DOR, BOO, BUL, MAR, and BO1. The two clusters have fixed differences at a minimum of 28% of their loci. Split decomposition analysis supports the southern cluster. The degree of genetic heterogeneity within both groups suggests the presence of multiple taxa.

Within the northern cluster, four allopatric groups are apparent: group 1 CUN-SUP-KOR-BEA, group 2 LAM-BOR, group 3 YAB-RR1-RR2, and group 4 BIL-SPI-WAS. Group 1 has fixed allelic differences with group 2 at three loci (*Acoh-2, Ca* and *Idh-1*), with group 3 at two loci (*Ca* and *Pgk*) and with group 4 at two loci (*Ca* and *Idh-1*). Within group 1, a single fixed difference at *Aldh* distinguishes CUN from BEA. Group 2 has fixed differences with group 3 at two loci (*PepD* and *Pgk*), and with group 4 at one locus (*Acoh-2*). However, LAM has fixed differences with group 4 at four additional loci (*Aat-2, Eno, Ldh-2, Mpi*) and BOR has fixed differences with group 4 at one additional locus (*G3pdh*). The minimum percentage fixed difference between group 2 and group 4 is 6%. Group 3 has fixed differences with the group 4 cluster at a minimum of two loci (*Acoh-2* and *PepD*). Split decomposition analysis supports groups 2 and 3.

The southern cluster comprises two genetic subgroups HYL-NEW-DOR-BO1 and BUL-BOO- MAR. BO2 is a single specimen, which is a probable F_1 hybrid between these two groups. The HYL-NEW-DOR-BO1 subgroup has one fixed difference in allopatry (*Aat-2*) with the BUL-BOO-MAR subgroup to the south. OTUs HYL and DOR, have an additional fixed difference (*Eno*) with BUL-BOO-MAR and OTU BO1 has two additional fixed differences (*Eno* and *G3pdh*) with BUL-BOO-MAR. Overall, there is an average percentage 5% fixed differences between HYL-NEW-DOR-BO1 and BUL-BOO-MAR.

To investigate the nature of possible interaction between the northern and southern subgroups within group 5, we carried out detailed collections in the Hastings River catchment from Mt Boss State Forest (SF) and three locations in Werrikimbe National Park (NP). These specimens were typed subsequently for the three informative loci, *Aat-2, Eno*, and *G3pdh*. Typing of the Mt Boss SF/ Plateau Beech specimens revealed them to be only the northern type; however, specimens from Cobcrofts and Gorge Creeks in Werrikimbe NP were a mixture of genotypes including southern, F_1 hybrids and F_2/backcross hybrid genotypes (Table 2). At the Gorge Creek location, electromorph frequencies at each of the three loci typed appear to be consistent with expectations under Hardy-Weinberg equilibrium (Table 2).

Table 1. Allele frequencies at 34 loci, expressed as a percentage, in 20 OTUs of *Philoria*. Alleles are designated alphabetically, in order of increasing electrophoretic mobility. Where enzymes are encoded by more than one locus, the loci are designated numerically in order of increasing electrophoretic mobility. Where the allele frequencies are not given, the frequency is 100%. Sample sizes are given at the head of each column. The loci, *Aat-1, Cap, Gtdh*, and *Lgl*, were invariant in all OTUs, while *Est* and *Ntak*, scored in OTUs 13 to 19 only, were also invariant.

OTU	**CUN**	**SUP**	**KOR**	**BEA**	**YAB**	**RR1**	**RR2**	**LAM**	**BOR**	**SPI**	**BIL**	**WAS**	**HYL**	**NEW**	**DOR**	**BO1**	**BUL**	**BOO**	**MAR**	**BO2**
locus	**5**	**8**	**8**	**4**	**6**	**2**	**3**	**1**	**5**	**8**	**3**	**2**	**7**	**4**	**4**	**4**	**3**	**1**	**3**	**1**
Aat-2	d(10) b(90)	d(31) b(69)	d(6) b(94)	b(50) a(50)	b	b	b	a	b(87) a(13)	d(25) b(75)	d(17) b(83)	d(25) b(75)	b	d(12) b(63) a(25)	b	b	c	c	c	c(50) b(50)
Acon-1	b	b(36) a(64)	b(33) a(67)	b(75) a(25)	b	e(25) b(75)	b	e(50) b(50)	d(50) b(25) a(25)	d(7) b(86) a(7)	b	b	c	c	c	c(87) b(13)	c	c	c	c
Acon-2	c	d(14) c(58) b(21)	c(43) b(57)	c(62) b(25) a(13)	d	d	e(33) d(67)	e	f(10) e(90)	c(94) b(6)	c(67) b(33)	c(75) b(25)	e	e	f(12) e(88)	f(25) e(75)	e	e(50) d(50)	e	e
Adh	a	a	a	b(37) a(63)	a	a	a	b(50) a(50)	b(60) a(40)	a	a	a	a	a	a	a	a	a	a	a
Aldh	b	b(57) a(43)	c(19) b(75) a(6)	a	b	b	b	b	b	b	b(50) a(50)	c(25) b(75)	c	c	c	c	c	c	c	c
Ca	a	a	a	a	b	b	b	b	b	c(62) b(38)	b	c(25) b(75)	a	a	a	a	a	a	a	a
Eno	b	b	b	b	b	b	b	a	b(80) a(20)	b	b	b	b	c(25) b(75)	b	b	c	c	c	c(50) b(50)
Fumh	c	c	c	c	c	c	c	c	c	c	c	c	b	b	b(87) a(13)	b	b	b	b	b
Fbp	b	b	b	b	b	b	b	b	b(70) a(30)	b	b	b	b	b	b	b	b	b	b	b
G3pdh	c	c	c	c	c	c	c	c(50) b(50)	b	c	c	d(25) c(75)	c(64) a(36)	c(37) a(63)	c(37) a(63)	c	a	a	a	a
Gpi	b(40) a(60)	c(6) b(94)	b	b	b	c(25) b(75)	b	b(50) a(50)	b(10) a(90)	b	b	b(75) a(25)	d(79) b(21)	b	d(17) b(83)	b	b	b	b	b
Iddh	b	b	b	b	b	b	b	b	b(12) a(88)	b	b	b	b	b	b	b	b	b	b	b
Idh-1	b	b	b	b	c(87) a(13)	c(50) a(50)	c(50) b(50)	c	c	c	c	c	c	c	c	c	c	c	c	c
Idh-2	d	d	e(6) d(94)	d	d	d	d	d	e(60) d(40)	d(94) c(6)	d	d(75) c(25)	b(36) a(64)	b	b	b	b	b	b	b
Ldh-1	a	a	a	a	a	c(25) a(75)	c(17) a(83)	a	a	a	a	a	b(7) a(93)	a	a	a	a	a	a	a
Ldh-2	b	b	b(94) a(6)	b	b(42) a(58)	c(25) b(75)	c(83) a(17)	c	c(30) b(60) a(10)	b	b	b	c	c(75) b(25)	d(12) c(88)	c(87) b(13)	c	c	c	c
Mdh-1	b(60) a(40)	b(31) a(69)	b(12) a(88)	b	b	b	b	b	b	b	b	b	c	c	c	c	c	c	c	c
Mdh-2	b	b	b	b	b	b	b	b	b	b	b	b	b	b(87) a(13)	b	c(12) b(88)	b	b	b	b
Mpi	e(20) c(30) b(50)	e(12) c(50) b(38)	e(19) c(56) b(25)	b	b	b	b	d	d(10) c(10) b(70) a(10)	b	b	b	d	d	d	d	d	d	d	d
PepA	b(50) a(50)	b(57) a(43)	b(33) a(67)	a	d(20) b(80)	d(75) b(25)	d(50) b(50)	b	b(90) a(10)	d(50) b(50)	b(50) a(50)	b	c	d(12) c(88)	c	d(12) c(88)	c	c	c	c
PepB	c(50) b(50)	c	c(31) b(69)	c	c	c	c	c	d(30) c(60) b(10)	c	c	c	b(86) a(14)	b(25) a(75)	b(87) a(13)	b	b	b	b	b
PepD	c(90) b(10)	c	d(12) c(75) b(13)	c	d	d	d	c	c	c	c	c	d(21) b(79)	b	b(87) a(13)	d(37) b(63)	b	b	b	d(50) b(50)
Pgam	a	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Pgdh	d(20) a(80)	d(19) a(81)	d(43) a(57)	d(62) a(38)	a	a	a	a	a	a	a	a	a	a	a	a	a	c(50) a(50)	c(25) a(75)	b(50) a(50)
Pgk	c(10) b(90)	b	c(7) b(93)	b	a	a	a	b	c(10) b(90)	b(50) a(50)	b(50) a(50)	b(75) a(25)	b	b	b	b(87) a(13)	b(33) a(67)	b	c(50) b(33) a(17)	b(50) a(50)
Pgm	b	b(94) a(6)	b	b	b	c(25) b(75)	b	b	b	b	c(33) b(67)	b	b	b	b	b	b	b	b	b
Sod	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	a	a	a	a
Tpi	a	a	b(6) a(94)	a	a	a	a	b(50) a(50)	b(17) a(83)	a	a	a	b	b	b	b	b	b	b	b(50) a(50)

Table 2. Genotype frequencies at three loci scored among *Philoria* from two locations in the Hastings River, NSW catchment. χ^2 test (one df) of departure from Hardy-Weinberg equilibrium genotype frequencies. All values were not significant at $\alpha = 0.05$.

locus	observed frequency Gorge Creek	χ^2	observed frequency Cobcrofts Creek	χ^2
Aat-2	aa 3, ab 11, bb 3	1.45	aa 1, ab 4, bb 1	3.65
Eno	aa 6, ab 7, bb 4	0.99	aa 1, ab 3, bb 2	3.33
G3pdh	aa 4, ab 7, bb 5	0.25	aa 3, ab 2, bb 0	3.80

Hennigian cladistic analysis of the allozyme electrophoretic data, in which group 5 was used as the outgroup to the northern cluster, revealed a number of unique alleles in each of the taxa identified among the northern OTUs of *Philoria*. Group 1 is characterized by unique alleles at *Acon-2*^{a}, *Ldh-2*^{a}, *Mdh-2*^{e}, *Pgam*^{d}, and *Pgk*^{a}; group 2 by unique alleles at *Eno*^{a}, *Fumh*^{a} and *Sod*^{a}; group 3 by unique alleles at *Iddh*^{a}, *Idh-2*^{c} and *PepD*^{b}, and group 4 by unique alleles at *Ca*^{c}, *G3pdh*^{d} and *Idh-1*^{c}. MP analysis found 2726 trees of length 170 steps. Bootstrapping with 2000 pseudoreplicates with the "fast heuristic search" option found support for monophyly of group 1 in 72% of pseudoreplicates, for group 3 in 64% of pseudoreplicates and for the northern cluster in 100% of pseudoreplicates. All other nodes received support from less than 50% of pseudoreplicates.

Mitochondrial nucleotide sequences. Specimens representing the geographic range of each group identified in the allozyme analysis were sequenced. Specimens from Levers Plateau, NSW (LEV) that were not available at the time the allozyme analysis was conducted were included in the nucleotide sequence analysis. The aligned *ND4* nucleotide sequences are available from GenBank, accession numbers are AY178866–901. A total of 616 aligned sites were available of which 272 were variable and 215 were parsimony informative. The most suitable model of nucleotide substitution for these data found with Modeltest was the Tamura-Nei model (Tamura & Nei, 1993) with a specified gamma shape parameter (Γ). Values estimated for parameters of this model were: base frequencies A 0.2629, C 0.3326, G 0.1256, T 0.2787; substitution rates $A\leftrightarrow C$ 0.739, $A\leftrightarrow G$ 14.16, $A\leftrightarrow T$ 0.917, $C\leftrightarrow G$ 0.787, $C\leftrightarrow T$ 4.55, $G\leftrightarrow T$ 1.0; $\Gamma = 0.294$.

An ML tree of the 23 haplotypes found among 26 individuals of *Philoria* sequenced is shown in Fig. 2B. In the MP analysis, 78 equally most parsimonious trees were found of length 543 steps. The strict consensus of the MP trees resembled the ML tree in showing the five major groups that were present in the allozyme analysis. Specimens from the LEV OTU clustered within group 2 (the *P. loveridgei* lineage). Monophyly of the haplotypes within four of the five groups is strongly supported by bootstrapping in both MP and ML analyses (bootstrap proportions greater than 70% *sensu* Hillis & Bull [1993]). The BOR-LAM-LEV (group 2) cluster is not strongly supported in any of the analyses but is nevertheless present in each analysis. Relationships among the five groups are not strongly supported, but some patterns are consistent among the analyses. All analyses place group 2 as the sister lineage to the remaining clusters, and groups 1, 3 and 4 are monophyletic. In contrast many relationships within each of the five groups are well supported (Fig. 2B). Of particular note is the presence of two divergent haplotype lineages within group 2. The deep divergence between LAM and BOR is also reflected by long terminal branches in the CSE NJ tree based on the allozyme data. In summary, the mitochondrial nucleotide sequence analyses are strongly congruent with the allozyme analyses in that both recover five groups that could be considered as distinct evolutionary lineages as they are supported with data from multiple independent genetic markers.

Morphological analysis. DFA was performed to assess whether each of the genetic groups could be distinguished on the basis of their body shape. Separate analyses were conducted for males and females. An initial DFA was conducted on the specimens that had either been identified *a priori* by allozyme electrophoresis or mitochondrial nucleotide sequencing or were from precise locations where other individuals had been identified from the genetic analyses. The latter action rests on the assumption that a single taxon is present at any one location. As only six *a priori* genetically identified specimens of group 2 were available for morphological analysis, we performed a second DFA including specimens from two other locations in the Border Ranges NP and Lamington NP where the genetically identified specimens had been sampled. This provided 10 additional females of *P. loveridgei*. Sample sizes and a *posteriori* percent correct classifications for the second analysis are presented in Table 3.

Table 3. *A posteriori* percent correct classifications of genetically defined groups (grp 1–5) in discriminant function analysis based on seven variables.

		DFA group assignment				
a priori group	% correct	grp 1	grp 2	grp 3	grp 4	grp 5
females only						
1	100	11	—	—	—	—
2	86	—	12	2	—	—
3	75	1	1	6	—	—
4	60	1	—	1	3	—
5	91	—	—	1	—	10
males only						
1	79	11	1	1	1	—
2	100	—	5	—	—	—
3	75	3	—	9	—	—
4	25	4	—	2	2	—
5	99	—	—	1	—	71

In a forward stepwise DFA of males only, 13 of 111 *a priori* classified cases (12%) were misassigned. Group 2 specimens were correctly assigned in 100% of cases. Classifications for groups 1, 3, 4 and 5 were poorer at 79, 75, 25 and 99% correct respectively. Six variables (TL, E, IN, HL, EN, SV) were retained in the model, with TL making the highest contribution to the first canonical variate. In a forward stepwise DFA of females only, 90, 93 and 100% of group 1, 2 and 5 cases respectively were correctly assigned. For groups 3 and 4, 80 and 67% of cases were correctly classified. Seven of the 49 *a priori* classified cases were misassigned. Group 1 specimens were all correctly assigned, while classifications for groups 2, 3, 4 and 5 were

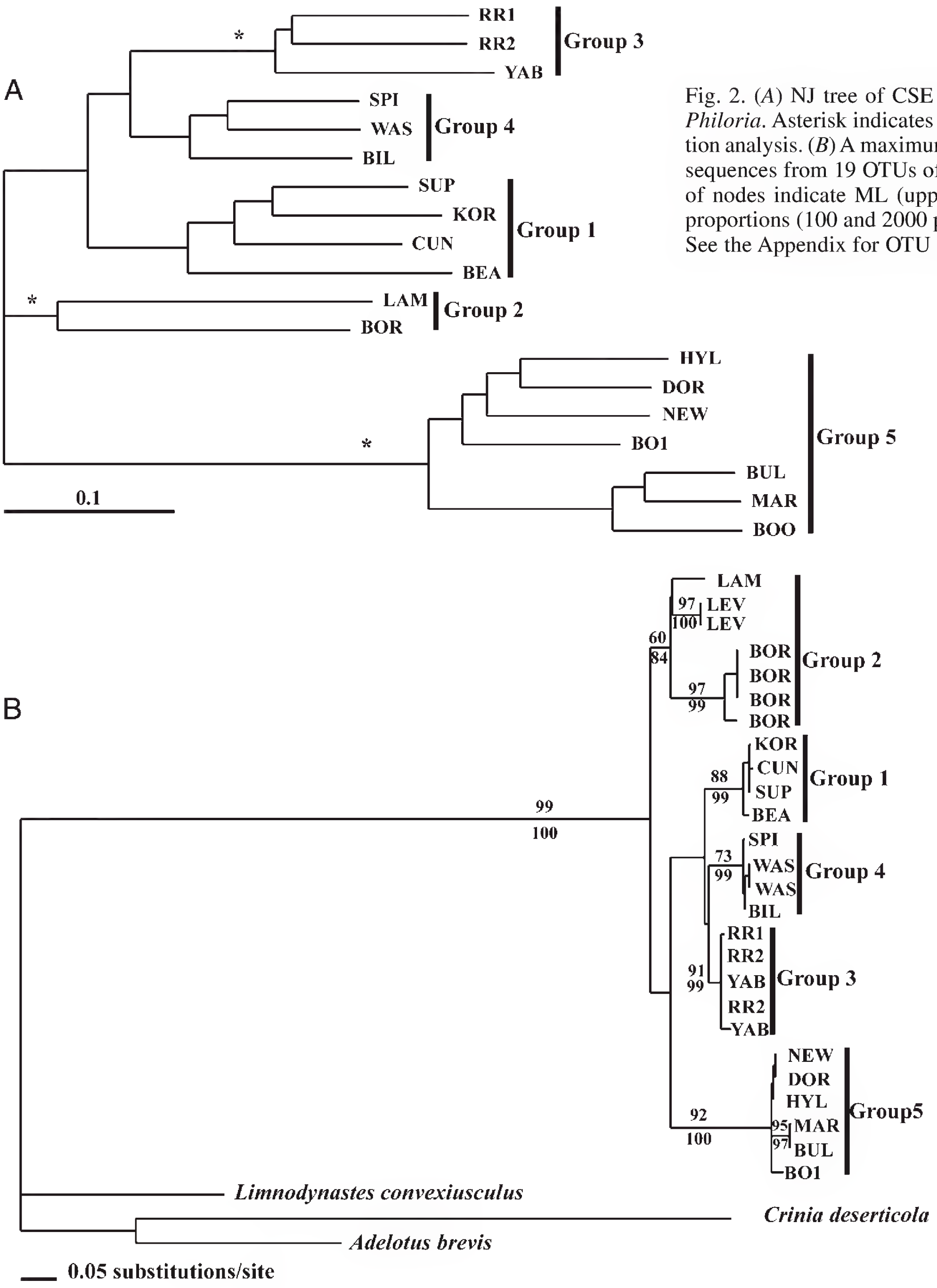

Fig. 2. (*A*) NJ tree of CSE distances among 19 OTUs of *Philoria*. Asterisk indicates support from split decomposition analysis. (*B*) A maximum likelihood tree of the 26 *ND4* sequences from 19 OTUs of *Philoria*. Numbers to the left of nodes indicate ML (upper) and MP (lower) bootstrap proportions (100 and 2000 pseudoreplicates respectively). See the Appendix for OTU abbreviations.

86, 75, 60 and 91% correct. Six variables (TL, IN, E, SV, HL, HW) were retained in the model, with TL making the largest contribution to the first canonical variate.

The type specimens of *P. kundagungan*, *P. loveridgei* and *P. sphagnicolus* were entered unassigned to any group. The DFA correctly assigned QM J 23944, the type of *P. kundagungan*, to group 1 with an *a posteriori* probability of 0.61, and AMS R16005 the type of *P. sphagnicolus* to group 5 with an *a posteriori* probability of 0.99. However, BM 1947.2.1994 the type of *P. loveridgei* was assigned to group 3 with *a posteriori* probability of 0.99, an unexpected finding given that the collection location is within the known range of group 2.

Mating call analysis. The mating calls of five genetic groups of *Philoria* comprise a single note (Table 4, Fig. 3). In most of the groups, the call starts with full energy and tapers off. There is a slight rise to dominant energy in groups 1 and 5.

On the basis of call duration and pulses per call, the genetic groups can be divided into two call types: groups 1 to 4 and group 5 (Table 4). The call of group 5 is approximately four times as long as the other species and the number of pulses per call is between 0.2 and 0.5 times greater and therefore the pulse repetition rate is slower in group 5. The dominant frequencies of the calls are also different, with group 5 having a fundamental frequency at

Table 4. Characteristics of the male advertisement call of the five genetic groups of *Philoria*. n = number of males analysed.

Group—OTU	n	temp (°C)	fundamental and minor component frequency (kHz)	mean call length (sec±SD)	mean call rate	number of pulses per call (range)	mean pulse rate±SD
1—SUP,KOR,BEA	3	11.5–13	0.59	0.1244	7.03	11.2 (10–12)	0.0109
2—BOR	2	15	0.51, 0.23	0.1381±0.025	5.35	9.7 (8–10)	0.0153±0.003
3—SPI	1	10	0.57	0.1232±0.006	6.75	9.5 (8–10)	0.012±0.001
4—RR1	2	na	0.59	0.1672±0.01	5.18	9.5 (9–10)	0.018±0.0003
5—NEW	3	11	0.63, 0.15	0.7301±0.119	8.81	21.5 (14–25)	0.037±0.002
5—DOR	6	12.1–17	0.74, 0.15	0.4945±0.069	8.61	19.3 (11–25)	0.027+0.004

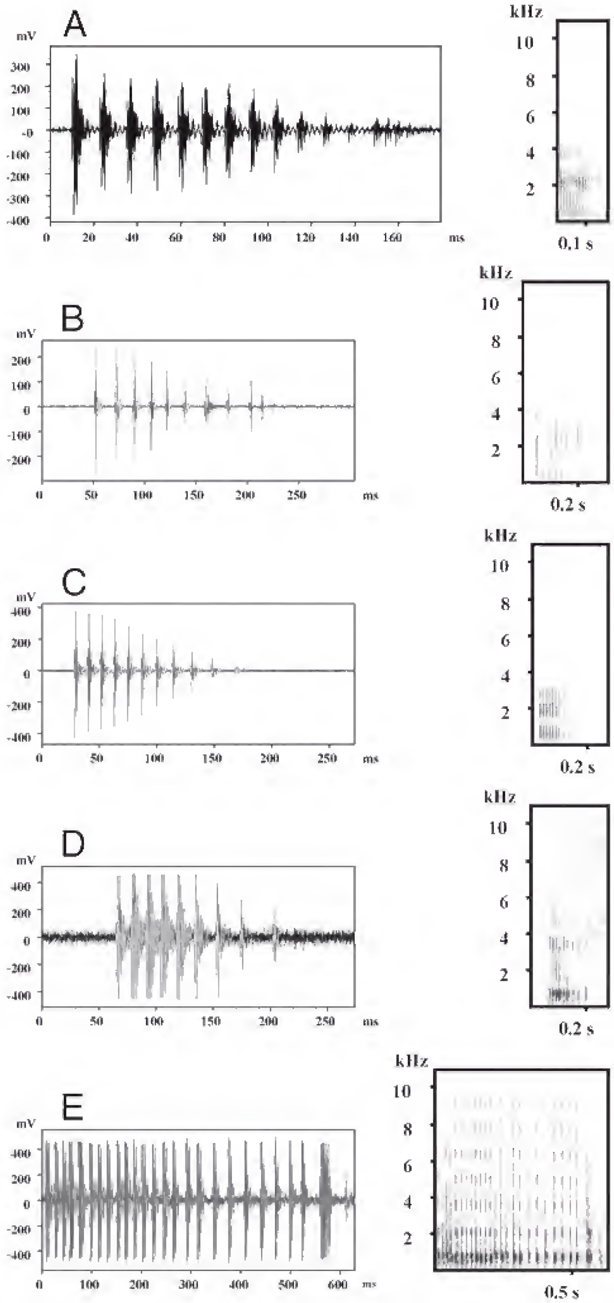

Fig. 3. Waveforms (left) and spectrograms (right) of a single male advertisement call of (*A*) *Philoria kundagungan* from Mount Superbus (SUP); (*B*) *P. loveridgei* from Border Ranges NP (BOR); (*C*) *P. pughi* from Spirabo SF (SPI); (*D*) *P. richmondensis* from Dome Mountain (RR1); and (*E*) *P. sphagnicolus* from Calacoma Falls (DOR).

0.9 kHz with a minor component at 1.6 kHz, while the other species have the fundamental frequency at 2.2 kHz, 2.0 kHz, 0.7 kHz, and 0.5 kHz respectively (Table 4).

The calls of groups 1 to 4 are similar in call duration and pulse repetition rate, but they differ in fundamental frequency (Table 4). Groups 3 to 4 have the fundamental frequency of their calls below 1 kHz with minor components at 0.7 and 0.5 kHz respectively, while group 1 has the fundamental frequency at 2.2 kHz, with minor components at 0.4 and 1.2 kHz. Group 1 has a call most similar to group 2 with the fundamental frequency at 2.0 kHz and a minor component at 0.5 kHz in the latter.

Rationale for recognizing species. Virtually any species concept (see Avise [1994] for a recent review) can be used to recognize the presence of phenotypically differentiated sympatric species where there is no hybridization or introgression. However, the basis which we will follow in this paper for the treatment of species boundaries among allopatric populations needs to be discussed. The evolutionary (ESC) and phylogenetic (PSC) species concepts, which rely on the recovery of the historical relationships of the organisms under consideration, have gained recent currency as the basis for the recognition of bisexual species as historical entities among allopatric or hybridising populations. However, the process of induction that allows recognition of species boundaries remains prone to a large degree of subjectivity, as no consensus exists as to how inclusive (PSC) or exclusive (ESC) historical entities should be that we would hypothesize to be lineages i.e., species (Frost *et al*., 1992). Furthermore, a well resolved "species tree" of recently diverged populations is often not achieved readily. In practice, allopatric populations that can be diagnosed by one or more apomorphic character states irrespective of their perceived potential for hybridization with closely related populations are often accorded specific status (Nixon & Wheeler, 1990; Davis & Nixon, 1992).

In the present study we used phylogenetic analyses of nuclear encoded allozymes and mitochondrial nucleotide sequences to define evolutionary lineages, as apart from comparisons involving *P. sphagnicolus*, none of the male advertisement call data or external morphology show non-overlapping variation. If indeed speciation in *Philoria* has been allopatric resulting from fragmentation of the historical range of the northern *Philoria* (as seems likely), then evidence of post-fragmentation evolution of the populations is required to substantiate an argument for the separate species status. This would be especially acute if the populations were thought to have been fragmented recently and to have been subject to divergence mainly through the effects of small population size, i.e., accelerated drift. Typically, if a large ancestral population was to be fragmented into smaller disjunct populations, small population size, if maintained for extended periods, would lead to an overall loss of diversity and greater geographic partitioning of the remaining diversity. Our molecular data demonstrate that the taxa have undergone significant evolution in allopatry as each is now reciprocally monophyletic for their mitochondrial genomes and each has a number of apomorphic allozyme alleles consistent with sufficient time having passed for post-isolation mutations to have appeared.

Consequently we present evidence for post-fragmentation divergence. While the type of molecular markers that we have assayed may not measure phenotypic divergence, especially as it pertains to traits that could influence directly reproductive compatibility (Ferguson, 2002), these markers can provide an array of evolutionary measures of genome-wide post-fragmentation divergence and in particular an array of diagnostic loci.

Dealing with the allozyme data first, one would expect that as populations recover from fragmentation (if indeed the scale of fragmentation had been such that the population fragments were small) new allozyme alleles would appear due to mutations. The rate of appearance of new alleles is dependent on the rate of mutation, selection and long-term population size. We note that each of the taxa of the cluster that includes groups 1, 3 and 4 have a number of alleles not found elsewhere in *Philoria*, i.e. these alleles are lineage-specific autapomorphies. We also note that at the loci that show fixed differences between taxa none of the alleles involved are lineage-specific and therefore their taxon distribution is likely to have been produced by random sorting (and drift) from the putative polymorphic widespread ancestral population.

Each of the taxa is monophyletic for its mitochondrial DNAs. Coalescence theory predicts that reciprocal monophyly for two populations will take $4N_e$ generations, where N_e is the effective population size. So the larger N_e the longer the time taken for reciprocal monophyly to be achieved. There is no *prima facie* evidence that populations of *Philoria* are small. The current range of each taxon encompasses a number of catchments and population sizes for at least three taxa, groups 1, 2 and 5 must number in the thousands, if not tens of thousands for group 5.

Lastly, mitochondrial genetic distances between taxa are of an order expected for sister species pairs of amphibians. The minimum distance between taxa of the cluster that includes groups 1, 3 and 4 is 5.4% uncorrected sequence divergence, which lies well within the range of values based on the mitochondrial *cytochrome b* gene (2.5% to 19%) for sister species pairs of amphibians surveyed by Johns & Avise (1998). Assuming that rates of change in vertebrate *ND4* are equivalent to that of another protein encoding mitochondrial gene, *cytochrome b* (ie 0.8 to 2.5% per Myr, summarized in Lougheed *et al.*, [1999]), separation of the minimally divergent mtDNA clades occurred some 2.16 to 6.74 Myr ago. These clades have been diverging at least since the early Pleistocene.

Within the cluster that includes groups 1, 3 and 4, populations within each taxon were sampled from a number of catchments and showed very low levels of mitochondrial diversity between samples contrasting with the substantially greater divergence between taxa. Thus samples from different catchments do not necessarily show high levels of divergence. Similarly, samples from different catchments from within the range of a taxon did not show fixed allozyme differences. These points indicate that genetic cohesion is not confined in its limits to single catchments, i.e. the smallest population units.

Subsequent phenetic analyses of multivariate morphometrics and male advertisement calls supported these lineages in part, i.e. the separation of *P. sphagnicolus* from the remaining taxa. In summary, on the basis of the genetic data, morphology and mating calls, the following species are recognized: group 1—*Philoria kundagungan* (Ingram & Corben, 1975), group 2—*P. loveridgei* Parker, 1940, group 3—*P. pughi* n.sp., group 4—*P. richmondensis* n.sp. and group 5—*P. sphagnicolus* (Moore, 1958).

Systematics

In addition to describing each of the new taxa, we also redescribe the existing taxa because of the limitations of the identification of *Philoria* species in New South Wales and Queensland with the presently available literature and the much larger number of specimens available since each of the taxa were described initially. The two new species described below are placed in the genus *Philoria* in the endemic Australian family Myobatrachidae, based on the diagnoses of Parker (1940) and Cogger (1992) and the genetic data presented herein.

Philoria loveridgei Parker, 1940

Type data. The holotype is an adult female (BM 1947.2.1994) collected in the McPherson Ranges, Queensland.

The type description lists the collection location of the holotype rather imprecisely as the "McPherson Ranges, 3–4000 ft, south Queensland" (Parker, 1940). Because the McPherson Ranges include the known range of *P. loveridgei* and extends close enough to the known range of *P. richmondensis* n.sp., we cannot be certain that the type was collected within the range of *P. loveridgei* as presently known. Furthermore, the DFA alone is not capable of precisely determining the species identity of any *Philoria* from far northeast New South Wales and Queensland which includes the McPherson Ranges. Therefore in the interest of maintaining nomenclatural stability we refer the holotype of *P. loveridgei* to group 2, the taxon which contains the populations to which this name has been traditionally applied. These populations include the eastern Border Ranges and Lamington National Parks.

Other material examined. See Appendix.

Diagnosis. Relatively small adult size (SVL to 32 mm); males with poorly developed nuptial pad on first finger; well-developed black head stripe; flanks either entirely black or with a black mark of variable size, and dorsum either brown, reddish-brown bronze or light grey.

Description. A small, squat, ground dwelling frog. Adult males (n = 15) measure 25 to 30 mm and females (n = 13) 27 to 32 mm SVL. Head shorter than wide (HL/HW mean 0.74, range 0.58–0.91). Head length approximately one-quarter snout-vent length (HL/SVL mean 0.26, range 0.20–0.31). Hind limbs short (TL/SVL mean 0.42, range 0.38–

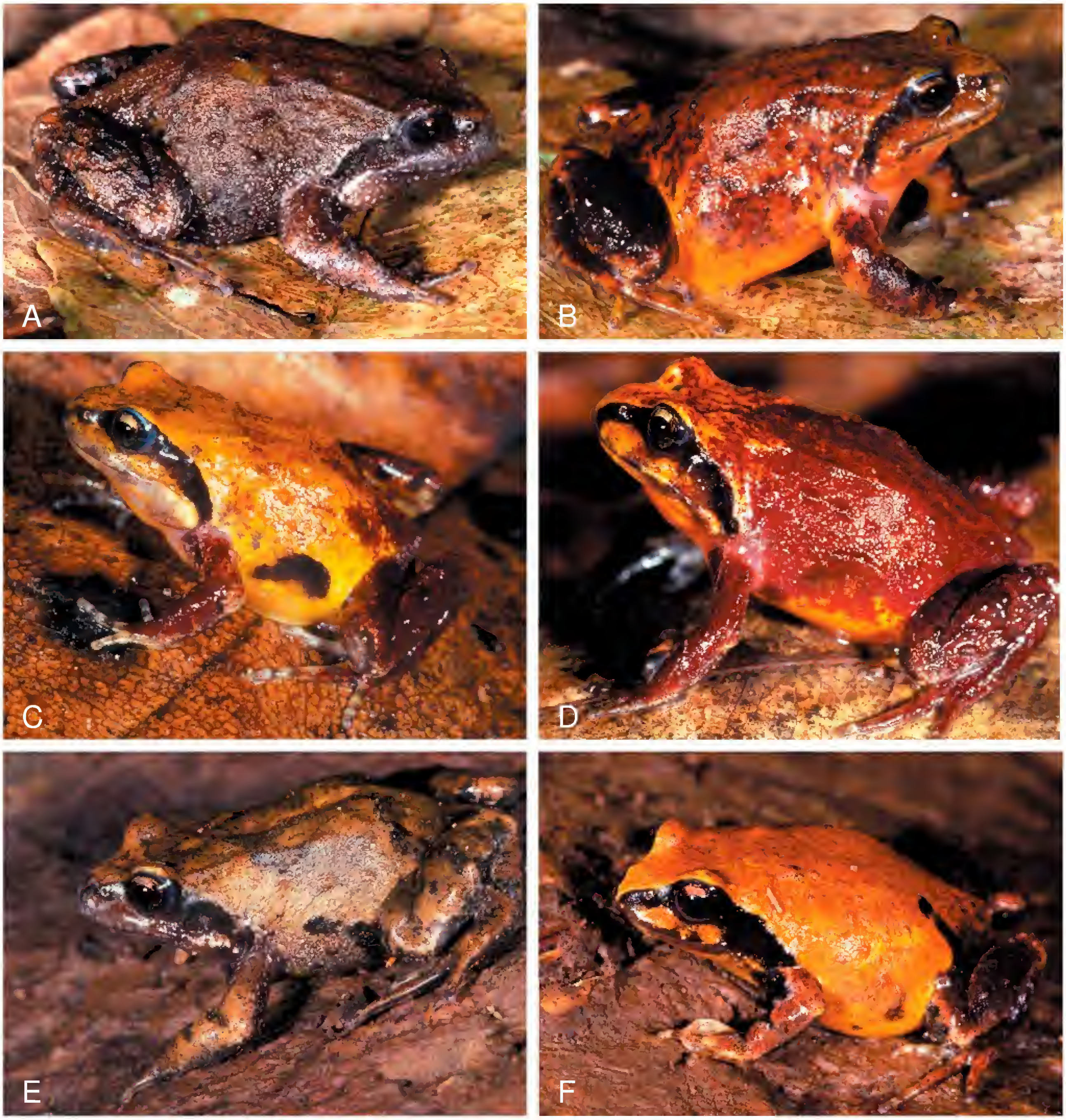

Fig. 4. Photographs of living specimens of: (*A,B*) *Philoria kundagungan*—adult males, Koreelah State Forest (KOR); (*C,D*) *P. pughi*—holotype, an adult male (AMS R152706), and an adult female (ABTC 25369) from Cedar Creek Trail, Washpool NP, NSW (WAS); (*E,F*) *P. richmondensis*—holotype, an adult male (AMS R152707), and an adult female (ABTC 25225) from Bungdoozle Road, Richmond Range NP, NSW (RR2).

0.47). Eye to naris distance to internarial ratio highly variable (EN/IN mean 0.58, range 0.38–0.69). Dorsal colour varies from light grey mid-dorsal area with black flanks and upper surfaces of limbs, to light brown with darker brown irregular patches to fawn with a few spots of darker pigment and a black or dark brown patch on the flank. Limbs sometimes with faint transverse bands. A dark brown or black stripe extending from the snout, through eye, to base of arm. Ventral surfaces usually uniformly pale but some individuals with light mottling on throat and undersurfaces of hindlimbs. Usually a pair of small dark marks either side of cloaca. Fingers in decreasing order of length 3>2>4>1. Toes in decreasing order of length 4>3>5>2>1. In males either no nuptial pad or a dark, very weakly developed nuptial pad on first finger. Spatulae on first and second fingers in females. Vomerine teeth extending to the level of the inner edge of the choanae. Tongue broad. Tympanum indistinct.

Dimensions of holotype (mm). SVL 29.9, HL 7.2, HW 10.5, TL 12.9, E 3.0, EN 1.3, IN 3.4.

Distribution and abundance. Ninety eight specimens are recorded in the Australian and Queensland Museums from 28 locations within one rainforest block which contains the Border Ranges, Lamington, Mt Warning and Nightcap National Parks (Barker *et al.*, 1995; AMS and QM registers, 1993).

Conservation status. Listed under Schedule 2 of the New South Wales *Threatened Species Conservation Act*, 1995 as vulnerable, and in the Queensland *Nature Conservation Act*, 1992 as rare. The reason for the listing in NSW is given as follows: "Population severely reduced; threatening processes severe; ecological specialist" (NSW NPWS, 1994). Whilst the combined area of the range of *P. loveridgei* is relatively small, a comparatively large number of populations are fairly evenly distributed throughout the range. Most of the range is protected within the national park estate. While only small populations were observed during the present study, Seymour *et al.* (1995) observed a number of large populations with choruses of over 10 calling males, in the summer of 1991–1992. Evidence of recruitment was found at all localities during their study. In view of the above, the conservation status of this species remains unchanged.

Philoria sphagnicolus (Moore, 1958)

Type data. The holotype is an adult male, AMS R16005, collected on 21 November 1952 at Point Lookout, New South Wales.

Other material examined. See Appendix.

Diagnosis. Relatively large adult size (SVL to 37 mm); usually with either an arrow shaped black band across lower back with apex towards head or two black patches on lower dorsum at an oblique angle over the ilium, and males with well-developed nuptial pad on first finger. Male advertisement call has a higher number of pulses per call and a longer call duration than other species of *Philoria* from NSW and Queensland.

Description. A small, robust, ground dwelling frog. Adult males (n = 91) measure 24 to 35 mm and females (n = 17) 29 to 37 mm SVL. Head shorter than wide (HL/HW mean 0.68, range 0.57–0.85). Head length approximately one-quarter snout to vent length (HL/SVL mean 0.25, range 0.20–0.30). Hind limbs short (TL/SVL mean 0.46, range 0.38–0.51). Ratio of eye to naris distance to internarial span variable (EN/IN mean 0.63, range 0.44–1.04). Dorsal colour varies from cream through various shades of yellow to orange, red or black usually with irregular spots or patches. Black patches on lower dorsum at an oblique angle over ilium, less frequently extending to and joining at midline in an arrow shape with apex directed anteriorly or, in about one third of specimens, lower dorsum is unmarked. Some dark specimens with a broad cream vertebral band. Dorsal skin usually smooth, occasionally with a few tubercules or short raised ridges along mid-dorsolateral area aligned along long axis of body. Ventral surfaces vary from white to orange often with darker brown to black mottling on abdomen, throat and undersurfaces of limbs. Palms vary from completely dark to completely pale but subarticular and palmar tubercules always pale. Soles completely dark but first and second fingers always pale. A brown or black stripe extending from nostril through eye to base of arm always present but variably developed. Flank with or usually without a black band. A horizontal black band extending laterally from over cloaca to ventral surface of thigh. Vomerine teeth posterior to and extending to inner edge of choanae. Fingers in decreasing order of length 3>2>4>1. Toes in decreasing order of length 4>3>5>2>1. Well-developed dark nuptial pad on first finger of males and a spatulae on each of first and second fingers of females.

Dimensions of holotype (mm). SVL 32.5, HL 9.0, HW 11.7, TL 14.4, E 2.8, EN 1.96, IN 3.64.

Distribution and abundance. The distribution of *P. sphagnicolus* extends along the eastern escarpment of the Great Dividing Range in northern NSW from the Marsh SF in the south northwards to Ramornie SF and the vicinity of Glen Innes (Fig. 5). Included in this distribution are four national parks (Werrikimbe, New England, Dorrigo and Bellinger River), two nature reserves (Mt Hyland and Mt Seaview), a number of timber reserves (Mt Banda Banda and Rimau Road) and several state forests (Brooklana, Marengo, Mistake, Mt Boss, Never Never, Nulla Five Day, Oakes, Ramornie, Styx River, and Wild Cattle Creek). The detection of *P. sphagnicolus* in Ramornie SF and just to the east of Glenn Innes represents substantial northern extensions to the range of the species. The Australian and Queensland Museums record 75 specimens from 18 localities, and the NEFBS supplied another location in the Bulga SF. A further 23 locations were found during the course of the present study in the following catchments: Rosewood River, Wild Cattle Creek, Never Never River, Bellinger River, Nymboida River, Forbes River and Hastings River.

The southern-most record of *P. sphagnicolus* with voucher specimens is Marsh SF Wotherspoon (1981) claimed a southern range extension for *P. sphagnicolus* from near the Barrington Tops Guest House, Barrington Tops NP with a report of large numbers of *P. sphagnicolus* foraging on rainforest leaf litter after two days of rain. We doubt the validity of this record for several reasons. Wotherspoon (1981) reported the SVL of one specimen as 52 mm. The largest vouchered specimen of *P. sphagnicolus* reported to date (this study) is 37 mm. Unfortunately, no voucher specimens or photographs were taken and Wotherspoon's is the only record of *P. sphagnicolus* from Barrington Tops NP. Additionally, the site was unlike any other where *P. sphagnicolus* has been found. It was not associated with a stream or running water, which is where large breeding congresses have been found. It is also the only report of *P. sphagnicolus* being observed "foraging on leaf litter". The present authors have never observed *P. sphagnicolus* in the open, but always under some form of cover. During the course of the present study, the site reported in Wotherspoon (1981) was visited after heavy spring rain and large numbers of *Lechriodus fletcheri* were observed moving around the leaf litter and at the edge of small ephemeral ponds on the forest floor. *Lechriodus fletcheri* is reasonably similar in appearance to *P. sphagnicolus* although it is much larger reaching a maximum recorded body length of 50 mm (Moore, 1961; Barker *et al.*, 1995; Cogger, 1992). The 52 mm specimen measured by Wotherspoon (1981) said to be of "average" size for the population, is 2 mm larger than the maximum size of *L. fletcheri* reported in the literature. This discrepancy aside, we consider it likely that *L. fletcheri* was mistaken for *P. sphagnicolus*. However, irrespective of whether *L. fletcheri* was the mistaken species, the evidence outlined above strongly suggests that the population reported by Wotherspoon (1981) was not *P.*

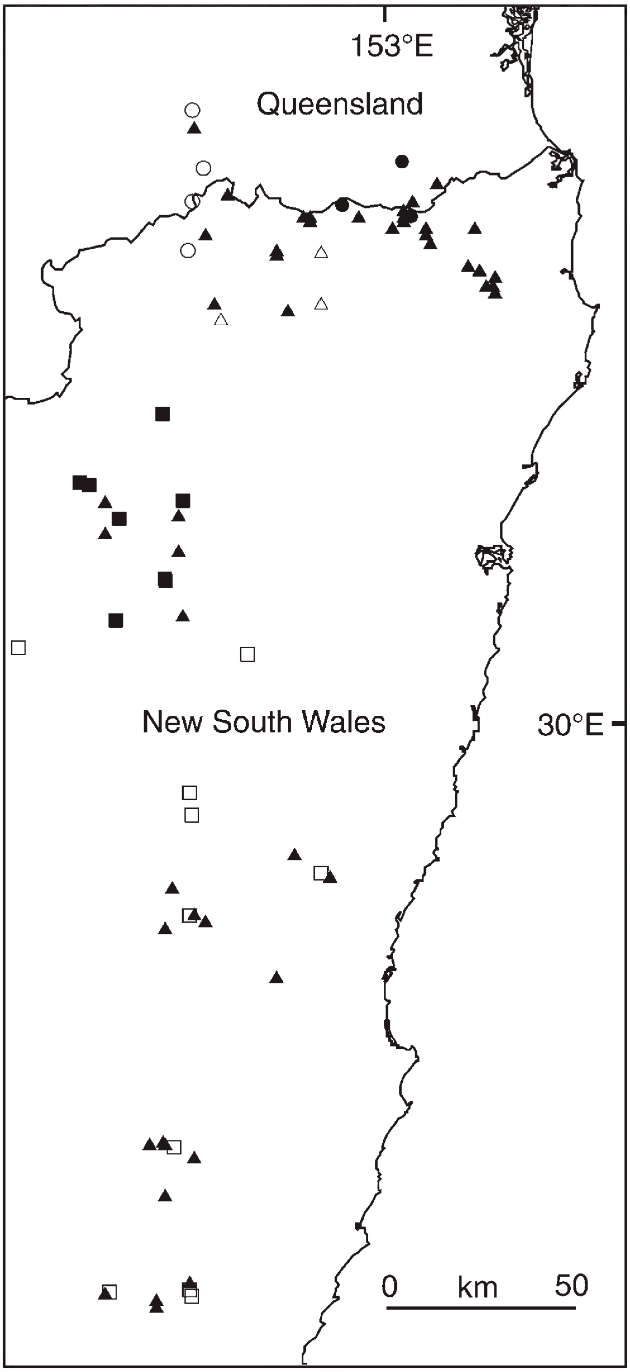

Fig. 5. Map showing distribution of *Philoria* in northern NSW and southeast Queensland based on museum vouchers. Symbols: ○ *P. kundagungan*, ● *P. loveridgei*, ■ *P. pughi*, △ *P. richmondensis*, □ *P. sphagnicolus*, ▲ species' identity not determined.

sphagnicolus. This report is therefore discarded in reviewing the distribution of the species.

Conservation status. Listed under Schedule 2 of the New South Wales *Threatened Species Conservation Act*, 1995 as vulnerable. The reason for the listing is as follows: "Population and distribution suspected to be reduced; threatening processes severe; ecological specialist". However, we consider *P. sphagnicolus* to be the most secure of the five taxa studied here for the following reasons:

a As a result of the present study *P. sphagnicolus* is known now from a total of 37 locations, more than double the 18 locations previously available in museum records.

b There appears to be substantial suitable habitat for *P. sphagnicolus* throughout its range. There are a great number of small rainforest streams originating at higher altitudes, and forming part of the four major catchments that drain from the Dorrigo and New England National Parks (Rosewood River, Bellinger River, Never Never River, Wild Cattle Creek). All of these represent potentially suitable habitat for *P. sphagnicolus*. A cause for concern however, is the potential for damage to the habitat of populations in the Wild Cattle Creek catchment through logging operations in Wild Cattle Creek SF Additionally, development such as clearing for agriculture and forestry has reduced the amount of higher altitude rainforest and this is likely to have decreased the species' abundance. *Philoria sphagnicolus* was observed to be in constant contact with water, hence any water pollution originating from agricultural practices affecting the headwaters of rainforest stream might also impact on local populations.

c There appear to be very few barriers to dispersal of *P. sphagnicolus* throughout its range, the majority of which falls in national parks with extensive wilderness areas. The escarpment between Dorrigo NP and New England NP is very steep and rugged and has a continuous cover of rainforest.

d Breeding congresses observed during the course of the present study were generally relatively small; seven locations had 10 or more calling males in a breeding congress, but two of these had 20 or more. These larger congresses were all observed during November after recent rainfall. Apart from populations of *P. sphagnicolus*, the largest breeding congress observed among the other species was eight calling males of *P. kundagungan* at Mt Superbus, Queensland.

The conservation status of the genetically distinctive southern populations of *P. sphagnicolus* needs further attention. Only six localities are known, four localities are recorded near Elands including the Boorganna Nature Reserve (NR), and one each from Bulga and Marsh State Forests. The largest breeding congress recorded during the course of the present study was at Bulga SF where six calling males were observed. Boorganna NR, the only location that is part of the national park estate, is a very small isolated rainforest pocket surrounded by cleared farmland. The other localities are either on freehold land or in state forests.

Philoria kundagungan (Ingram & Corben, 1975)

Type data. The holotype is an adult female, QM J23944, collected by C.J. Corben and A.K. Smyth on 3 January 1974 at Mistake Mountains, Queensland, 27°53'S 152°21'E.

Other material examined. See Appendix.

Diagnosis. Relatively small adult size (SVL to 28 mm); dark head stripe absent or, if present, narrow; abdomen usually either yellow or red with smaller patches of either colour, and males with poorly developed nuptial pad on first finger (Fig. 4).

Description. A small squat frog with a robust, pear-shaped body. Adult males (n = 15) measure 23 to 28 mm and females (n = 15) 23.5 to 28 mm SVL. Head shorter than wide (HL/HW mean 0.69, range 0.62–0.79). Head length approximately one-quarter snout to vent length (HL/SVL mean 0.24, range 0.21–0.28). Hind limbs short (TL/SVL mean 0.41, range 0.38–0.46). Ratio of eye to naris distance to internarial span variable (EN/IN mean 0.63, range 0.54–0.71). Dorsal surface varies from either yellow, orange, bright red to black with patches of alternative colours. In about half of specimens, a pair of raised ridges is present on dorsum, starting behind eye and continuing posteriorly about a third of way along dorsum. Dorsal skin either smooth or with raised "warts", with frequency of "warty" specimens increasing to the south. Ventral surface variably immaculate yellow, yellow with red patches on either throat, abdomen or lateral aspects of abdomen, or yellow with red and brown patches with latter speckled with fine white dots. Undersurfaces of limbs range from yellow to yellow with red or brown wash, latter with small irregular shaped white marks. A black patch over cloaca only or a black patch over cloaca and adjacent upper thighs or entire upper thighs. Fingers and toes unwebbed. Tympanum indistinct. A dark facial stripe is present in about half the specimens running from near tip of snout, through loreal region below canthus rostralis, crossing eye to base of forelimb. Fingers in decreasing order of length 3>2>4>1. Toes in decreasing order of length 4>3>5>2>1. Nuptial pad on first finger of males weakly developed. Spatulae on first and second fingers of females. Vomerine teeth behind level of choanae.

Dimensions of holotype (mm). SVL 23.5, HL 6.8, HW 8.75, TL 9.35, E 2.7, EN 1.5, IN 1.45.

Distribution and abundance. Found along the ranges from the Mistake Mountains west of Brisbane south to Beaury SF approximately 15 km S of the New South Wales–Queensland border (Ingram & Corben, 1975; AMS and QM registers, 1993). The species is known from 27 specimens from only eight localities. Although Ingram & Corben (1975) make no reference to the abundance of *P. kundagungan*, the small number of known localities and specimens suggest that it is not common. No new locations were found for *P. kundagungan* during the course of the present study.

Conservation status. Listed as rare under the Queensland *Nature Conservation Act 1992,* and under Schedule 2 of the New South Wales *Threatened Species Conservation Act*, 1995 as vulnerable. It has a much smaller range than both *P. loveridgei* and *P. sphagnicolus*; it is known from fewer locations, and less specimens have been deposited in museum collections (Ingram & Corben, 1975; Queensland Museum records, 1993; Australian Museum records, 1993). It is known for certain from only eight locations within a very small range. Only three of the known localities, Mistake Mountains NP, Mt Superbus Main Range NP and Cunninghams Gap NP, all in Queensland, are within the national parks estate. All other localities are in state forests. Recruitment was observed at the four locations sampled in the present study. The major threat is likely to be loss or damage to habitat through logging operations. During field work for the present study, logging was observed in the immediate vicinity to *P. kundagungan* habitat at Beaury and Koreelah SF, NSW

Philoria pughi n.sp.

Type data. HOLOTYPE AMS R152706, an adult male from Cedar Creek Trail, Washpool National Park, New South Wales, 29°28'52"S 152°19'05"E (grid reference 4339 67385, zone 56), collected by Ross Knowles on 12 December 1992 (Fig. 4). PARATYPES: SAMA R39818–20 Billilimbra SF, collected by Ross Knowles on 6–8 December 1991; AMS R165008–10 Spirabo SF collected by Ross Knowles on 30 November 1992; AMS R165013 Spirabo SF collected by Ross Knowles on 29 October 1992; SAMA R39241 Spirabo SF collected by Harry Hines on 29 January 1990; AMS R165014 Cedar Creek, Washpool NP collected by Ross Knowles on 12 December 1992.

Other material examined. See Appendix.

Diagnosis. Relatively small adult size (SVL to 30 mm); males with poorly developed nuptial pad; well-developed facial stripe present, and dorsum usually yellow, red or maroon, occasionally light tan or bronze, usually with conspicuous black patch on flank.

Description. Body robust, pear-shaped. Head shorter than wide (HL/HW 0.64), head length approximately one quarter of SVL (HL/SVL 0.23). Snout blunt in profile. Nostrils more lateral than superior, closer to snout than to eye. Distance between eye and naris half that of internarial span (EN/IN 0.58). Canthus rostralis well defined and concave. Eye relatively large, its diameter greater than eye to naris distance (E/EN 1.5). Pupil shape horizontal when constricted. Tympanum small and indistinct. Tongue approximately rectangular. Vomerine teeth in two laterally aligned plates, separated in midline, behind level of choanae.

No webbing on fingers or toes. Digits long, slender and cylindrical. Inner and outer palmar tubercules small but distinct. Fingers in decreasing order of length 3>2>4>1. Very weakly developed nuptial pad on first finger. Hindlimb short (TL/SVL 0.44). Toes in decreasing order of length 4>3>5>2>1. Inner metatarsal tubercule at base of first toe small but distinct. No outer metatarsal tubercule. Dorsum and abdomen smooth.

Dimensions of holotype (mm). SVL 25.4, HL 5.8, HW 9.1, EN 1.8, IN 3.6, E 2.7, T 11.1.

Colour in life. Dorsum orange fading to yellow on flanks with small flecks of maroon. Crescent shaped black mark on mid-flank. Loreal region dark. A black band expanding posteriorly from snout through nostril along canthus rostralis, through eye along side of head to base of forearm. Blue sclera around eyes. Upper surfaces of limbs maroon, colour extending onto lower abdomen above vent. In preservative, abdomen pale, submandibular area and ventral surfaces of limbs, soles and palms, outer fingers and toes dark. Other fingers and toes with light banding.

Variation. Adult males (n = 6) measure 25 to 30 mm and females (n = 7) 27 to 30 mm SVL. Head shorter than wide (HL/HW mean 0.72, range 0.65–0.84). Head length approximately one-quarter snout to vent length (HL/SVL mean 0.24, range 0.22–0.30). Hind limbs short (TL/SVL mean 0.42, range 0.38–0.47). Ratio of eye to naris distance to internarial span variable (EN/IN mean 0.63, range 0.55–0.75). Dorsum either smooth or with raised ridges (aligned along long axis of body) or tubercules along mid-dorsal line and flanks. The description of variation of colour in life is based on colour transparencies of six specimens. Dorsum varies from either plain orange or orange with dark irregular shaped and sized patches and spots or plain maroon. Upper surfaces of limbs maroon. Crescent shaped black mark on mid-flank present in a majority of specimens. Black patch over cloaca, sometimes spreading onto thighs. Ventral surfaces yellow with red patches on abdomen, undersurfaces of hindlimbs mostly red or yellow with numerous red patches. Spatulae on first and second fingers of females.

Etymology. Named for Dailan Pugh (North East Forest Alliance), for his contributions to the protection of the habitat of the species.

Distribution. Confirmed records from seven localities in the Gibraltar Range, Girard, Billilimbra, Forestland, and Spirabo State Forests, and Gibraltar Range and Washpool National Parks to the west of Grafton. The NEFBS (1993) recorded this species from four other localities on the basis of morphological appearance and geographic location. However, these records should be treated with caution as our records include populations of *P. sphagnicolus* in this region. The Australian and Queensland Museums hold specimens from a further eight locations in this area: 20 km SE Tenterfield, the Cangai, Gibraltar Range, Spirabo SF and Washpool SF and Washpool NP. These are probably referable to *P. pughi* on the basis of geographic proximity to OTUs assigned by molecular analyses, but definite assignment awaits genetic analysis. An attempt to sequence *ND4* from AMS R132319 from Cangai SF, 40 km W Grafton was unsuccessful.

Conservation status. The distribution of *P. pughi* is much smaller than the previously recognized distributions of either *P. kundagungan* or *P. loveridgei,* to which this species had been attributed in the past. Only the Gibraltar Range NP and Washpool NP populations are protected within the national park estate with records from 7–12 sites and four other possible but unconfirmed sites. The four populations examined during the present study were all very small. The largest number of calling males observed at any one location was six, at Spirabo SF where the species was found in the boggy headwaters of a small creek. At this site the creek bed had been trampled by cattle in the exact area in which the nests of *P. pughi* were found. Whilst no assessment has been carried out of the potential damaging effects of this trampling on the population's breeding area, the eggs of this species are large and relatively fragile, and would be likely to be damaged or destroyed by trampling by stock.

Philoria richmondensis n.sp.

Type data. HOLOTYPE AMS R152707, an adult male from Bungdoozle Road, Richmond Range National Park, New South Wales, 28°39'19"S 152°42'38"E (grid reference 4717 68357, zone 56), collected by Ross Knowles on 28 October 1992 (Fig. 4). PARATYPES: AMS R165031–3, SAMA R57464 Little Haystack Ck, Yabbra SF collected by Ross Knowles on 3 December 1992; AMS R165028–9 Dome Mountain, Richmond Range SF collected by Ross Knowles on 28 Oct. 1992; AMS R165030, SAMA R57463 Bungdoozle Road, Richmond Range SF collected by Ross Knowles on 27 October 1992.

Other material examined. See Appendix.

Diagnosis. Relatively small adult size (SVL to 28 mm); well-developed head stripe present; dorsum usually yellow, red or maroon, occasionally light tan or bronze; usually without conspicuous black patch on flank; usually with black patches on lower dorsum at an oblique angle over the ilium, and males with poorly developed nuptial pad on first finger.

Description. Body robust, pear-shaped. Head long (HL/HW 0.64), head length approximately one quarter SVL (HL/SVL 0.23). In profile snout prominent and blunt. Nostrils more lateral than superior, closer to snout than to eye. Distance between eye and naris just over half that of internarial span (EN/IN 0.58). Canthus rostralis well defined and concave. Eye relatively large, its diameter greater than eye to naris distance (E/EN 1.5). Pupil shape horizontal when constricted. Tympanum small and indistinct. Tongue approximately rectangular. Vomerine teeth in two laterally aligned plates, separated in midline, behind level of choanae.

No webbing on fingers or toes. Digits long, slender and cylindrical. Inner and outer palmar tubercules small but distinct. Fingers in decreasing order of length 3>2>4>1. Nuptial pad on first finger weakly developed. Hindlimb short (TL/SVL 0.44). Toes in decreasing order of length 4>3>5>2>1. Inner metatarsal tubercule at base of first toe small but distinct. No outer metatarsal tubercule. Dorsum and abdomen smooth.

Dimensions of holotype (mm). SVL 25.4, HL 5.8, HW 9.1, EN 1.8, IN 3.6, E 2.7, T 11.1.

Colour in life. Dorsum bronze, with irregular black band across lower back and fainter black blotches on upper dorsum posterior to eyes and either side along spine. Loreal region dark. A black stripe from snout through nostril along canthus rostralis, through eye along side of head to base of forearm. Eyes with blue sclera. Lips slightly darker bronze than dorsum to brown. Black patches on posterior half of flank between arm and leg. Upper surfaces of limbs bronze with black transverse bands. In preservative, abdomen pale, submandibular area and ventral surfaces of limbs, soles and palms, outer fingers and toes dark. Other fingers and toes with light banding. Cloaca and upper thighs uniformly dark.

Variation. Adult males (n = 8) measure 24 to 28 mm and females (n = 5) 24 to 27 mm SVL. Head shorter than wide (HL/HW mean 0.71, range 0.64–0.82). Head length approximately one-fifth snout to vent length (HL/SVL mean 0.24, range 0.22–0.28). Hind limbs short (TL/SVL mean 0.41, range 0.38–0.47). Eye to naris distance to internarial ratio variable (EN/IN mean 0.63, range 0.55–0.72). Dorsum smooth. The description of variation of colour in life is based on colour transparencies of six specimens. Dorsum varies from bronze or brown to plain orange or orange with a few, small, dark marks or with occasional to numerous dark speckles. Most specimens have black patches on lower dorsum at an oblique angle over ilium, less frequently joining at midline to form an arrow shape with apex directed anteriorly. Upper surfaces of limbs bronze or brown. In some specimens arms with faint transverse black bands. Spatulae on first and second fingers of females.

Etymology. Named after the Richmond Range area that contains the entire distribution of the species.

Distribution. Known with certainty from only three locations within one continuous forest block within the

Richmond Range NP west to Yabbra NP The Australian and Queensland Museums hold several specimens from Bungdoozle Road, Richmond Range NP, Yabbra NP and Toonumbah SF that are likely to be examples of *P. richmondensis* on the basis of their geographic proximity to localities with genotyped specimens. The Australian and Queensland Museums also hold specimens from a number of localities that are geographically intermediate between the distributions of *P. kundagungan, P. loveridgei* and *P. richmondensis*. Assignment of these populations awaits genetic analysis.

Conservation status. *Philoria richmondensis* has a very small range and is known definitely from only three localities and possibly another three. The largest number of calling males observed (three) at any locality was at Dome Mountain, Richmond Range NP At both Bungdoozle Road, Richmond Range NP and Yabbra NP, no calling males were observed, but animals were located by turning leaf litter, logs and rocks. These searches were carried out in the months of October and December on field trips where breeding choruses of *P. kundagungan, P. pughi*, and *P. sphagnicolus* were observed at other locations. However, evidence of recruitment was found at both Dome Mountain, Richmond Range NP and Yabbra NP, in the form of nests with either eggs or tadpoles. It is likely that clearing for agriculture and forestry in the area surrounding its current distribution has substantially reduced the range of *P. richmondensis*. Urgent attention is needed to assess more fully its conservation status.

Habitat and reproductive biology of *Philoria*

The habitat and reproductive biology of all five species of *Philoria* are so similar that we can describe these features in general and note any exceptions.

Habitat. The potential range of *Philoria* in northeastern New South Wales and southeastern Queensland has now been surveyed extensively, in particular by the NEFBS in the early 1990s. *Philoria* species are distributed along the top of the eastern escarpment of the Great Dividing Range where cool temperate or sub-tropical rainforest occurs above 550 m elevation. Distinct gaps in the distribution can be seen in the drier and warmer Macleay Gorges region, southeast of Armidale, and the Guy Fawkes and Mann wilderness area, southwest of Grafton.

The habitat of all six species is similar (Ingram & Corben, 1975; Barker *et al.*, 1995; Anstis, 1981; Webb, 1989). All species are found predominantly in the boggy headwaters of rainforest streams and around soaks on the rainforest floor. Breeding pairs of all species mate in well-covered sites such as in small chambers excavated in mud and under rock or leaf litter, under the banks of small creeks, or in the sphagnum mat of bogs. Some populations of *P. sphagnicolus* also utilize cracks in rock faces for their nests (Moore, 1958). The predominant feature of all breeding habitats is the saturated state of the substrate.

Reproductive biology. *Philoria kundagungan* breeds from late August to mid February when males call from water-filled cavities under rocks or leaf litter. The eggs of 3.1 mm in diameter are contained in jelly capsules of 4.9 mm diameter. Eggs are laid directly in a foam nest in water-filled cavities (Ingram & Corben, 1975). *Philoria loveridgei* breeds from November to January, with males constructing smooth-walled chambers in the ground, which are moist but contain no free water (Moore, 1961; Ingram & Corben, 1975; Seymour *et al.*, 1995). Males may be found calling from these chambers, which can be very close to one another anywhere on the forest floor, especially along creeks (Ingram & Corben, 1975; Moore, 1961, Seymour *et al.*, 1995). Eggs in their individual jelly capsules are deposited in the chambers in a sticky, liquefied jelly mass. Unlike the other species there is no foam mass in the chamber. The eggs contain enough yolk to nourish the developing individual to the juvenile stage, hence the larvae do not have a truly aquatic stage (Moore, 1961). We recorded calling males and eggs of *P. pughi* from October to December. Males called in small congresses of up to six individuals. Males of *P. richmondensis* were heard calling in October (a single congress of three males), but eggs were found in October and December. *Philoria sphagnicolus* forms breeding congresses closely associated with creeks (Anstis, 1981). Breeding occurs from October to January with males calling during the day from established nest sites. Egg masses are of the foam type with the jelly mass closely packed with eggs (Moore, 1961). Water has been observed trickling through nest sites. Anstis (1981) speculated that *P. sphagnicolus* may exhibit some form of parental care as both males and females are often found beside a nest of eggs.

The reproductive biology of *Philoria* is unusual in that the embryos complete their entire development and metamorphosis within a nest in the ground. The tadpoles do not leave the nest until they emerge as metamorphlings and derive all their nourishment from the yolk that was contained in the egg. While in the nest, the tadpoles move through a jelly substance that is excreted into the nest by the female at the time of egg-laying (Seymour *et al.*, 1995). Herein lies a significant distinction between the nesting behaviour of *P. loveridgei* and the other species. With the exception of *P. loveridgei,* all of the nests that were observed where the eggs were at early stages of development were found to have foaming egg masses (Table 5). The foam is derived from the jelly substance secreted by the females with the eggs and is beaten with large spatulae on her fingers (Anstis, 1981; Seymour *et al.*, 1995). The foam egg mass provides adequate oxygen for the early stage embryos. Over time, the foam loses its bubbles to become a still jelly. Foam nests were observed up to Gosner's Stage 22–24. All nests with more advanced tadpole stages contained still jelly. *Philoria loveridgei* was observed to have a still jelly nest even when the embryos were in a very early stage of development (Table 5). Seymour *et al.* (1995) found that embryos at the bottom of nests of *P. loveridgei* were deprived of oxygen and eventually died. However, in subsequent stages of development, tadpoles periodically moved to the surface of the jelly and lashed their tails to produce an oxygen rich jelly around them.

Anstis (2002) indicates that the tadpole of *P. loveridgei* (Gosner stage 35) has substantially reduced tail fins and increased tail venation in comparison with *P. sphagnicolus* (Gosner stage 36) and *P. kundagungan* (Gosner stage 33). Comparable observations are not available for *P. pughi* and *P. richmondensis*.

Table 5. Field observations of foam status and number of eggs in 35 nests of *Philoria*. Data for *P. loveridgei* are from Seymour *et al.* (1995).

species	locations	number nests	nest jelly foam	Gosner's Stage	mean number eggs
Philoria kundagungan	Cunninghams Gap NP	1	jelly	>35	44
	Mt Superbus NP	1	foam	12–14	51
	Beaury SF	2	foam	22–24	32.5
	Koreelah SF	6	foam	15–17	47.5
Philoria loveridgei	Border Ranges NP	14	jelly	0–40	31.9
Philoria pughi	Spirabo SF	4	foam	5–7	40.5
	Washpool NP	1	foam	15–17	42
Philoria richmondensis	Richmond Range NP	1	jelly	34–35	36
	Yabbra SF	2	foam	15–17	50
Philoria sphagnicolus	Dorrigo NP	2	foam	5–7	37
	Marsh SF	1	jelly	38–40	—

Discussion

Despite the clear genetic discrimination among the four northern species of *Philoria*, these taxa show overlapping ranges of variation in both colour and pattern and in body shape as expressed by multivariate metric analysis Their male advertisement calls are also virtually indistinguishable. As an indication of the difficulty in distinguishing the northern *Philoria* species, neither of the photographs of *P. kundagungan* or *P. loveridgei* in Barker *et al.* (1995), the latest guide to Australian frogs, are consistent with the species descriptions or the identification key that accompany them. At present the best guide for species identification within *Philoria*, aside from genotyping, is geographic location, assuming of course that none of the taxa occur sympatrically. Unfortunately this approach does not help to resolve the species identity of a number of populations around the periphery of the range of *P. pughi* and some others that occur between populations of *P. kundagungan, P. loveridgei* and *P. richmondensis*. These may be additional populations of the described taxa or they may represent undescribed taxa. Determination of their identity is a matter of some urgency as at least one of these populations is within land proposed for an extension to a mining development.

Within *P. sphagnicolus*, there is evidence of two groups with relatively distinct mitochondrial haplotype lineages and differentiated across most of their geographic range by a single consistent fixed difference. Evidence of hybridization apparently with random mating patterns was found in a series of locations in the middle of the range of *P. sphagnicolus*. At present we lack comparative call data for the southern group and our knowledge of geographic distributions and degree of genetic introgression is too incomplete to allow a full assessment of the two groups" taxonomic status.

Key to the genus *Philoria*

1 Sides and back above vent with numerous tiny tubercules; usually a conspicuous parotid gland; large adult size (to 45 mm) .... *P. frosti*

—— Sides and back above vent smooth; no conspicuous parotid gland; smaller adult size (to 35 mm) 2

2 Intermediate adult size (32 to 37 mm); males with well-developed nuptial pad; usually with either an arrow-shaped black band across lower back with apex towards head or two black patches on lower dorsum at an oblique angle over the ilium; found south of 30°29'S .... *P. sphagnicolus*

—— Small adult size (27 to 30 mm); males with poorly developed nuptial pad; lower back without distinct black band or patches on lower dorsum; found north of 29°28'S 3

3 Head stripe absent or if present then narrow; abdomen usually either yellow or red with smaller patches of other colour .... *P. kundagungan*

—— Head stripe well developed; abdomen not yellow or red with smaller patches of other colour 4

4 Dorsum brown, reddish-brown, bronze or light grey; flanks entirely black or with a black mark of variable size .... *P. loveridgei*

—— Dorsum usually yellow, red or maroon, occasionally light tan or bronze; flanks with a distinct medial black mark or a continuation of the dorsal colouration 5

5 Flank usually with conspicuous black patch .... *P. pughi*

—— Flank usually without conspicuous black patch; found only in Richmond Range area .... *P. richmondensis*

This key may be of limited value in the event of further populations of *Philoria* are discovered in the northern part of their range in NSW and in southeastern Queensland. An accurate identification may only be possible through genetic methods.

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Appendix

Specimens of *Philoria* examined. Institution codes: *ABTC*, Australian Biological Tissue Collection, South Australian Museum, Adelaide; *AMS*, Australian Museum, Sydney; *QM*, Queensland Museum, Brisbane; *SAMA*, South Australian Museum, Adelaide. OTU codes are in upper case bold; * indicates specimens sequenced for mitochondrial DNA and typed for allozymes; ^{m} indicates specimens sequenced only for mitochondrial DNA and unmarked specimens were typed only for allozymes. All specimens used in genetic comparisons were examined morphologically.

Philoria kundagungan: **BEA** Kangaroo Ck, Beaury State Forest AMS R165031–5*; **CUN** Cunninghams Gap National Park (NP) AMS R165136–8,9*,40; **KOR** Acacia Plateau, Koreelah State Forest (SF) ABTC25303 [juvenile], AMS R165127*–30, SAMA R39238–40; **SUP** Mt Superbus AMS R165120*–3,5, 165141, ABTC25292–3. *Philoria loveridgei*: **LAM** Lamington NP AMS R165027*; **BOR** Border Ranges NP AMS R133242^{m}, 138936*,38–39,42*,59*; **LEV** Levers Plateau ABTC26285^{m}/7^{m}. *Philoria pughi*: **BIL** Billilimbra SF SAMA R39818,19*,20; **SPI** Spirabo SF ABTC25208, AMS R165008,9*,10–13, ABTC25359 [larva], SAMA R39241; **WAS** Cedar Creek, Washpool NP AMS R152706*, 165014*. *Philoria richmondensis*: **YAB** Little Haystack Ck, Yabbra SF AMS R165031–33^{m}, SAMA R57464*, ABTC25351, 72630–1; **RR1** Dome Mountain, Richmond Range SF AMS R165028–9*; **RR2** Bungdoozle Road, Richmond Range SF AMS R152707*, 165030, SAMA R57463. *Philoria sphagnicolus*: **HYL** Mt Hyland Nature Reserve (NR) AMS R165015, 165063–4, 165075, ABTC25204–6*; **NEW** Weeping Rock, New England NP AMS R165083, 165068*–9, ABTC24918; **DOR** Rosewood River catchment, Dorrigo NP AMS R165065–7*; **BO1/2** Cockerwombeeba Creek, Mt Boss SF AMS R165099–103, 165052–3, 165062, 165079–80*; King Fern Falls, Werrikimbe NP AMS R165019, 165049, 165098, 165110–21, ABTC12757; Cobcrofts Creek, Werrikimbe NP AMS R165104–6, 165018, 165048, 165088; Gorge Creek, Werrikimbe NP AMS R165022–4, 165045/7, 165055–8, 165085–7/89–92; **BUL** Ellenborough River, Bulga SF AMS R165017–9*; **BOO** Mumfords Creek, Boorganna NR AMS R165078; **MAR** Dingo Creek, Marsh SF AMS R165072*/77, 165118.

Outgroup sequences from GenBank: *Adelotus brevis* GenBank ABR268701; *Crinia deserticola* CDE269697; *Limnodynastes convexiusculus* LCO269707.

Additional specimens genotyped for "short" *ND4* fragment: (AMS) *Philoria pughi*—Cedar Ck, Gibraltar Range NP R96794–6; Girard SF R137756–7; Forestland SF R139030/6; Gibraltar Range R31694; Billilimbra SF R139510. *Philoria sphagnicolus*—Marengo SF R145663; Ramornie SF R145674.

Morphology only: (AMS) *Philoria kundagungan*—Cunninghams Gap R38193–4; Koreelah SF R133244; Beaury SF R130862. *Philoria loveridgei*—Wiangarie SF R68515–16/20/22–3/26/28, 86326; Border Ranges R131885–6, 131891, 133242. *Philoria pughi*—Washpool SF R96914. *Philoria richmondensis*—Dome Mountain R132432, 132454/7; Yabbra SF R130902. *Philoria sphagnicolus*—Dorrigo NP R20497, 32164–7, 66208; Point Lookout R20947; 17 km E Glenn Innes R32177; New England NP R15738–9, 17162, 20499–500, 71313–6; Elands R93690–1; Boorganna NR R93692; Mt Boss SF R79069, 108707–8, 108730–1/7/9, 108759; Marengo SF R145663.

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The Subfamily Littorininae (Gastropoda: Littorinidae) in the Temperate Southern Hemisphere: The Genera *Nodilittorina, Austrolittorina* and *Afrolittorina*

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ABSTRACT. The littorinine gastropods of the temperate southern continents were formerly classified together with tropical species in the large genus *Nodilittorina*. Recently, molecular data have shown that they belong in three distinct genera, *Austrolittorina, Afrolittorina* and *Nodilittorina*, whereas the tropical species are members of a fourth genus, *Echinolittorina. Austrolittorina* contains 5 species: *A. unifasciata* in Australia, *A. antipodum* and *A. cincta* in New Zealand, and *A. fernandezensis* and *A. araucana* in western South America. *Afrolittorina* contains 4 species: *A. africana* and *A. knysnaensis* in southern Africa, and *A. praetermissa* and *A. acutispira* in Australia. *Nodilittorina* is monotypic, containing only the Australian *N. pyramidalis*. This paper presents the first detailed morphological descriptions of the African and Australasian species of these three southern genera (the eastern Pacific species have been described elsewhere). The species-level taxonomy of several of these has been confused in the past; *Afrolittorina africana* and *A. knysnaensis* are here distinguished as separate taxa; *Austrolittorina antipodum* is a distinct species and not a subspecies of *A. unifasciata*; *Nodilittorina pyramidalis* is separated from the tropical *Echinolittorina trochoides* with similar shell characters. In addition to descriptions of shells, radulae and reproductive anatomy, distribution maps are given, and the ecological literature reviewed.

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The Littorinidae are among the most intensively studied families of marine gastropods and their systematics has been the subject of much research. As new techniques and tools have become available over the past 30 years, systematists have applied them to littorinids, with the result that the classification of the group has been repeatedly updated and refined. As late as 1970, the classification used by Rosewater (1970) was one in which both species and genera were defined principally by features of their shells. In the following decade the use of reproductive anatomy, morphometrics and electrophoresis began to result in recognition of new species (Heller, 1975; Hannaford Ellis, 1979). Information from scanning electron microscopy of radulae, light microscopy of sperm and from fine dissection was soon employed to redefine the traditional genera (Bandel & Kadolsky, 1982; Reid, 1986), and a cladistic analysis of the family was attempted (Reid, 1989). This served as the basis of a phylogenetic classification that has since become current in the systematic literature. Direct sequencing of DNA is now routine, and molecular phylogenetic trees have been produced for a few littorinid clades, notably the genera *Littorina* (Reid *et al*., 1996) and *Tectarius* (Reid & Geller, 1997). Recently, the phylogeny and classification of the subfamily Littorininae was tested with DNA-sequence data, resulting in significant changes to the scheme (Williams *et al.*, 2003). Although changing concepts of littorinid species and genera may be confusing to non-systematists, these refinements represent progress towards a phylogenetic system in which definitions of species will be informed by genetics as well as morphology, and generic groupings will accurately reflect evolutionary relationships.

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Among the littorinids most affected by changing classifications are those that have become familiar under the generic name *Nodilittorina* (Bandel & Kadolsky, 1982; Reid, 1989). The taxonomic history of this group is complex (Reid & Geller, 1997; Reid, 2002*a,b*; see Taxonomic History below). The name was introduced as a subgenus, for those *Littorina* species with nodulose shell sculpture, paucispiral operculum and unmodified aperture (von Martens, 1897). It was first treated as a genus by Abbott (1954) who, in the first anatomical account, noted close similarity with some *Littorina (Melarhaphe)* species with smooth, striate shells. Nevertheless, Rosewater (1970) retained an essentially shell-based generic classification, placing only nodulose species in *Nodilittorina*. Species with smooth shells were retained in the large genus *Littorina*, although he created the new subgenus *Austrolittorina* for those with penial anatomy resembling *Nodilittorina*. With increasing emphasis on the significance of radulae and anatomy, shell sculpture was recognized as a poor guide to relationships, and *Austrolittorina* was synonymized with *Nodilittorina* (Bandel & Kadolsky, 1982). It was not clear that this was a natural group, for in a cladistic analysis of available morphological characters only one non-unique synapomorphy was discovered, the colour pattern of the cephalic tentacles (Reid, 1989). However, this classification was widely adopted. The most recent review listed 60 members of *Nodilittorina*, the great majority of them distributed in the tropics (Reid, 2002b). A parsimony analysis of morphological characters of all known *Nodilittorina* species produced a poorly resolved tree, but suggested that a group of nine or ten species, all occurring in the temperate regions of the southern hemisphere, shared the apparent synapomorphy of an additional loop of the egg groove through the capsule gland in the pallial oviduct (Reid, 2002b). Furthermore, this "southern-temperate group" was reconstructed as sister to the northern-temperate genus *Littorina*, and nested within *Nodilittorina*. This implied that *Nodilittorina* was not a monophyletic clade, but because the phylogenetic reconstruction was based on relatively few available characters, the conclusion was tentative.

The suggestion of a group of southern-temperate *Nodilittorina* species was of more than purely phylogenetic and taxonomic importance. The species involved (two from southern Africa, four from Australia, two from New Zealand, two from the Pacific coast of South America) are abundant members of the littoral fauna, well studied by marine biologists (review by McQuaid, 1996a,b). Their possible relationship raised interesting biogeographic questions of the origin of similarities among the marine organisms of the southern continents. Furthermore, a possible sister-relationship with *Littorina* implied an antitropical distribution pattern. The phylogeny of the entire subfamily Littorininae was therefore reexamined with DNA-sequence data, with surprising results (Williams *et al.*, 2003). The genus *Nodilittorina* was shown to be polyphyletic, consisting of four distinct clades (Fig. 1) that must be recognized as genera (because they are of equivalent rank to other well established littorinid genera). The largest of these (*Echinolittorina*) is composed of more than 50 species of almost entirely tropical distribution. The southern-temperate species fall into three groups: one distributed in Australia, New Zealand and South America (five species of *Austrolittorina*), a second in southern African and Australia (four species of *Afrolittorina*) and a third in Australia alone (the monotypic *Nodilittorina sensu stricto*). As a consequence of these changing ideas of classification and phylogenetic relationship, the common Australian species "*Littorina*" *unifasciata* has, in just over 30 years, been variously classified as *Littorina (Melarhaphe), Littorina (Austrolittorina), Nodilittorina* and *Austrolittorina*. Recent generic assignments are summarized in Table 1.

Significant changes have also taken place in the species-level classification of the southern-temperate littorinines (Table 1). The most recent monographic treatment of the Indo-West Pacific Littorininae was that of Rosewater (1970). His species concepts were broad and based to a large degree on resemblances among shells. At least two nodulose species of *Echinolittorina* were included in his description of *Nodilittorina pyramidalis*, as pointed out by Reid (1989, 1992). Rosewater considered *Littorina* unifasciata to be a

Table 1. Summary of generic classification of southern-temperate Littorininae and species that have been confused with them. Generic and subgeneric abbreviations used in this table: *Af.*, *Afrolittorina*; *Au.*, *Austrolittorina*; *E.*, *Echinolittorina*; *L.*, *Littorina* (but subgenus *Littoraria* not abbreviated); *N.*, *Nodilittorina*.

species	Rosewater (1970)	Reid (1989)	Reid (2002a)	Williams *et al.* (in press)
pyramidalis	*N. pyramidalis pyramidalis*	*N. (N.) pyramidalis*	*N. pyramidalis*	*N. pyramidalis*
trochoides	*N. pyramidalis pyramidalis*	*N. (N.) trochoides*	*N. trochoides*	*E. trochoides*
pascua	*N. pyramidalis pascua*	*N. (N.) pascua*	—	*E. pascua*
unifasciata	*L. (Au.) unifasciata unifasciata*	*N. (N.) unifasciata*	*N. (Au.) unifasciata*	*Au. unifasciata*
fernandezensis	*L. (Au.) unifasciata fernandezensis*	*N. (N.) fernandezensis*	*N. (Au.) fernandezensis*	*Au. fernandezensis*
antipodum	*L. (Au.) unifasciata antipodum*	*N. (N.) antipodum*	*N. (Au.) antipodum*	*Au. antipodum*
cincta	*L. (Au.) cincta*	*N. (N.) cincta*	*N. (Au.) cincta*	*Au. cincta*
araucana	*L. (Au.) araucana*	*N. (N.) araucana*	*N. araucana*	*Au. araucana*
africana	*L. (Au.) africana*	*N. (?E.) africana*	*N. (Au.) africana*	*Af. africana*
knysnaensis	*L. (Au.) knysnaensis*	*N. (?E.) ?africana*	*N. (Au.) knysnaensis*	*Af. knysnaensis*
praetermissa	*L. (Littoraria) praetermissa*	*N. (?N.) praetermissa*	*N. (Au.) praetermissa*	*Af. praetermissa*
acutispira	*L. (?Littoraria) acutispira*	*N. (?N.) acutispira*	*N. (Au.) acutispira*	*Af. acutispira*

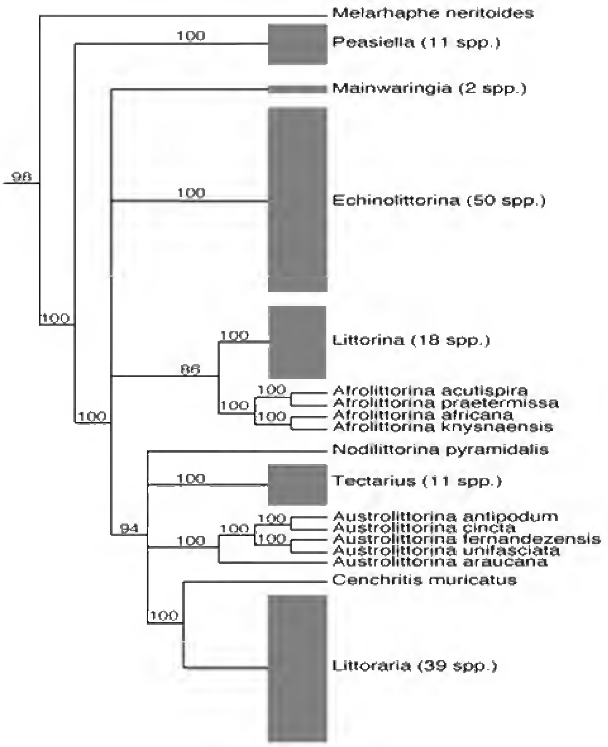

Fig. 1. Summary of molecular phylogeny of Littorininae, with species-level relationships shown for *Austrolittorina* and *Afrolittorina*, produced by Bayesian analysis of combined sequence data from 28S, 18S, 12S and COI genes; nodes supported by posterior probablities less than 85% have been collapsed. Redrawn from Williams *et al.* (2003). Numbers of species are totals of known species for each genus (Williams *et al.*, 2003, used fewer taxa as exemplars of these genera, but they are believed to be monophyletic); other genera are monotypic as shown.

temperate Pacific species with subspecies *unifasciata, antipodum* and *fernandezensis* in Australia, New Zealand and the Juan Fernández Islands respectively; these were later listed as distinct species of *Nodilittorina*, but without discussion (Reid, 1989). New data on egg-capsule morphology (Rudman, 1996) and a full description of *N. fernandezensis* (Reid, 2002*a*) supported this decision. The status of the two southern African species has also been disputed. Rosewater (1970) recognized both *Littorina africana* and *L. knysnaensis*, but these were later synonymized (Hughes, 1979; doubtfully by Reid, 1989), before once more being listed as distinct (Reid, 2002b). Of the ten southern-temperate littorinine species considered here, the definitions of only three have remained unchanged since the monograph of Rosewater (1970; see also Ponder & Rosewater, 1979) (*Austrolittorina cincta, Afrolittorina praetermissa, Afrolittorina acutispira*). Furthermore, anatomical characters of eight of the species have not been adequately described and illustrated; only *Austrolittorina fernandezensis* and *A. araucana* have received a full anatomical description (Reid, 2002*a*).

The aim of the present study is to present the first full descriptions of the eight southern-temperate littorinines that are poorly known anatomically, and to clarify their status as distinct species. These are *Nodilittorina pyramidalis, Austrolittorina unifasciata, Austrolittorina antipodum, Austrolittorina cincta, Afrolittorina africana, Afrolittorina knysnaensis, Afrolittorina praetermissa* and *Afrolittorina acutispira*. This will confirm the morphological characters of the genera *Nodilittorina, Austrolittorina* and *Afrolittorina* that were recently defined as a result of a molecular phylogenetic analysis (Williams *et al.*, 2003). In addition, the large taxonomic and ecological literature on these species will be reviewed and detailed distribution maps given. For completeness, diagnoses of the two remaining species of *Austrolittorina* are included (*A. fernandezensis* and *A. araucana*), although these have been fully described elsewhere (Reid, 2002*a*).

General discussion of the comparative morphology, biogeography and evolutionary radiation of these groups can be found in Reid (2002b) and Williams *et al.* (2003). Although the genera *Austrolittorina* and *Afrolittorina* have been clearly shown to be monophyletic clades by the analysis of DNA-sequence data, their relationships (and those of the monotypic *Nodilittorina pyramidalis*) with other littorinine genera remain poorly resolved (Williams *et al.*, 2003). It is, however, possible that the southern oceans have been a focus for the evolution of littorinines, and that these genera are not merely offshoots of a predominantly tropical radiation, contradicting earlier ideas (Reid, 1989). It is unfortunate that none of the three genera considered here has a pre-Pleistocene fossil record, so that hypotheses of their biogeographic history remain speculative. Based on imprecise molecular estimates of age, Williams *et al.* (2003) suggested that the family Littorinidae was older than had been supposed, and that *Austrolittorina* and *Afrolittorina* were ancient genera that were present on the shores of Gondwana as early as the Upper Cretaceous. This remains to be tested by the discovery of new fossil material.

Material and methods

This study is based on examination of all material in the collections of the following institutions: Australian Museum, Sydney (AMS), Natural History Museum, London (BMNH), National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), Muséum National d'Histoire Naturelle, Paris (MNHNP), Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB), Zoölogisch Museum, Amsterdam (ZMA) and National Museum of Wales, Cardiff (NMW). Additional material has been examined on loan from the following: Natal Museum, Pietermaritzburg (NM), South African Museum, Cape Town (SAM) and Museum of New Zealand Te Papa Tongarewa, Wellington (MNZ). All available primary type material from these institutions was examined, and also from Tasmanian Museum and Art Gallery, Hobart (TMAG), Staatliches Museum für Naturkunde Stuttgart (SMNS) and Oxford University Museum (OM). Other (almost entirely secondary) type material is housed in additional museums: Natur-Museum Senckenberg (SMF), Swedish Museum of Natural History, Stockholm (SMNH), Museum of Comparative Zoology, Harvard University (MCZ) and Auckland Museum (AM), but was not examined. Personal collections were made in South Africa (1970–1972), Australia (1980–1984), New Zealand (1981) and Chile (1998), and are deposited in BMNH. In total, 650 samples were examined of the eight species described here in detail (for the two additional members of *Austrolittorina, A. araucana* and *A. fernandezensis*, see Reid, 2002*a*).

Shell dimensions were measured with vernier callipers to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, and the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. Shell shape was quantified as the ratios H/B and H/LA (relative spire height, SH), and the range of these ratios is given. The parietal area adjacent to the aperture may show evidence of dissolution by the mantle edge, producing a crescentic eroded area. In descriptions of shell sculpture, primary grooves are incised spiral lines or grooves that are visible on the early teleoconch whorls. On the spire the primary grooves are counted between successive sutures, but on the last whorl they are counted from the suture to the periphery of the whorl (so that one or more extra grooves are visible). If the periphery is not well marked, grooves are counted over the entire last whorl, from suture to base. If present, secondary grooves appear by interpolation, usually on the penultimate or final whorl. The spaces between the grooves are referred to as ribs, whether or not they are strongly raised. Microstriae are fine incised spiral lines that cover the entire surface and are visible only under low magnification. The periphery is the junction between the upper part of the final whorl and the base of the shell; is usually marked by a slight angulation, or by an enlarged rib. The suture generally runs one or two ribs above the periphery, or is situated at the peripheral rib. Protoconchs are rarely preserved; where possible the whorls were counted as described by Reid (1996). The opercular ratio describes the coiling of the operculum, and is the ratio of two parallel measurements, the diameter of the spiral part divided by the maximum length (Reid, 1996).

Living animals were relaxed in 7.5% (volume of hydrated crystals to volume of fresh water) magnesium chloride solution. Animals were fixed in 10% seawater formalin buffered with borax, and stored in 80% ethanol. The most important anatomical characters for taxonomic purposes are the penis and oviduct; drawings of these were made by camera lucida and drawing conventions are indicated in Fig. 3. For general accounts of the anatomy of littorinids see Reid (1986, 1989, 1996). Sperm samples were removed from the seminal vesicles of relaxed, living animals, fixed in 0.5% seawater formalin, examined immediately by light microscopy, and drawn by camera lucida. Alternatively, sperm were removed from specimens fixed and stored in formalin, but not from material stored in ethanol (in which shrinkage of paraspermatozoa by about 20% occurs, Reid, 1996).

Radulae are relatively uniform in these littorinine species (with the exception of *Afrolittorina acutispira*) and therefore not useful for identification. At least three radulae were examined from each species. The relative radular length is the total radular length divided by shell height. Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 5 min, rinsed in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination with a scanning electron microscope. Unworn portions of the radula were viewed in three orientations: in standard flat view from vertically above the radula (to show shapes of tooth bases), at an angle of 45° from the front end (to show shape of tooth cusps), and at an angle of 45° from the side (to show relief). The shape of the rachidian (central) tooth was quantified as the ratio of the total length (in flat view) to maximum basal width. Numbers and relative sizes of cusps are not given for the five central teeth in each row, because these do not vary: three cusps on rachidian (largest central); four cusps on each of lateral and inner marginal (largest is third from inside in each case). All species show flanges on inside and outside of base of outer marginal tooth.

Synonymies are not exhaustive, but attempt to list all new names (including nomina nuda) and new combinations, major taxonomic works and faunistic lists, standard identification guides, and significant morphological descriptions. One lectotype has been designated in a case where syntypes were not conspecific, and one figure has been designated as lectotype for a valid name.

Distribution maps were plotted from the material examined, with the addition of literature records as indicated, where these extend the known range and were considered reliable. Localities are listed only when they are range limits or are of other biogeographic significance. Complete locality lists are available from the authors on request.

Systematics

Littorinidae Anon., 1834

Nodilittorina von Martens, 1897

Littorina (Nodilittorina) von Martens, 1897: 204 (type *Littorina pyramidalis* Quoy & Gaimard, 1833, by subsequent designation, Abbott, 1954: 451).

Taxonomic history. The name *Nodilittorina* was introduced by von Martens (1897) as a subgenus for those *Littorina* species with nodulose shell sculpture, but lacking the many-whorled circular operculum and apertural tooth characteristic of *Tectus* (now *Tectarius*, see Reid & Geller, 1997). In the influential classification of Thiele (1929; followed by Wenz, 1938; Clench & Abbott, 1942), *Nodilittorina* appeared as a subgenus of *Tectarius*, because of the narrow rachidian tooth. It was first used as a full genus by Abbott (1954), on the basis of comparisons of penes, radulae and egg capsules of *Nodilittorina tuberculata* (Menke, 1828) (now *Echinolittorina tuberculata*) with those of other littorinids. He did also note the "*Nodilittorina*-like" penes of *Littorina (Melarhaphe) mauritiana* (Lamarck, 1822) (a misidentification of *Austrolittorina unifasciata*, see synonymy of that species below) and *L. (M.) ziczac* (Gmelin, 1791) (now *Echinolittorina ziczac*), in the first indication that *Nodilittorina* might include species without nodulose shells. Nevertheless, in his monograph of Indo-Pacific species, Rosewater (1970) still emphasized shell sculpture above anatomical characters, and included only species with nodulose or granulose sculpture in *Nodilittorina*. Smooth-shelled species with penes resembling those of *Nodilittorina* (i.e. with single mamilliform gland and adjacent glandular disc, in terminology of Reid, 1989) were placed in a new subgenus, *Littorina (Austrolittorina)*. The first attempt to revise the classification of littorinids taking into account all available anatomical evidence was by Bandel & Kadolsky (1982). The main features of their diagnosis of *Nodilittorina* were: spirally striate, nodulose or granulose shell; pale basal band in aperture; narrow rachidian tooth; pelagic egg

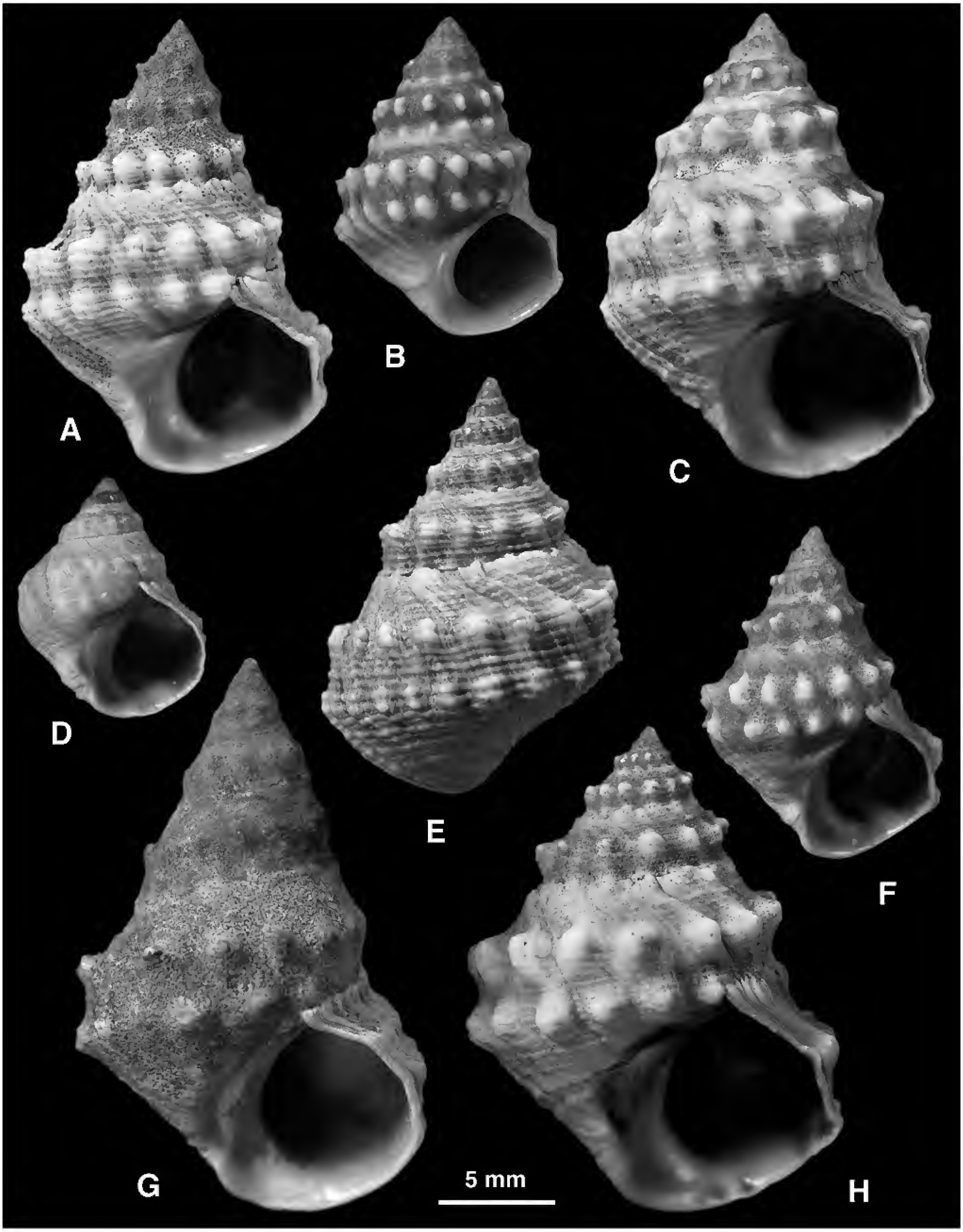

Fig. 2. *Nodilittorina pyramidalis*: (*A*) Jervis Bay, NSW, Australia (BMNH 1928.4.30.55). (*B, F*) Great Keppel Island, Queensland, Australia (AMS C089660). (*C*) Karuah, NSW, Australia (BMNH 20030388). (*D*) Alexandra Headland, Queensland, Australia (BMNH 20030389). (*E*) Long Reef, Collaroy, NSW, Australia (AMS C177413). (*G*) Lectotype of *Littorina pyramidalis* Quoy & Gaimard, 1833; Jervis Bay, NSW, Australia (MNHNP unreg.). (*H*) Lord Howe Island (AMS C089673).

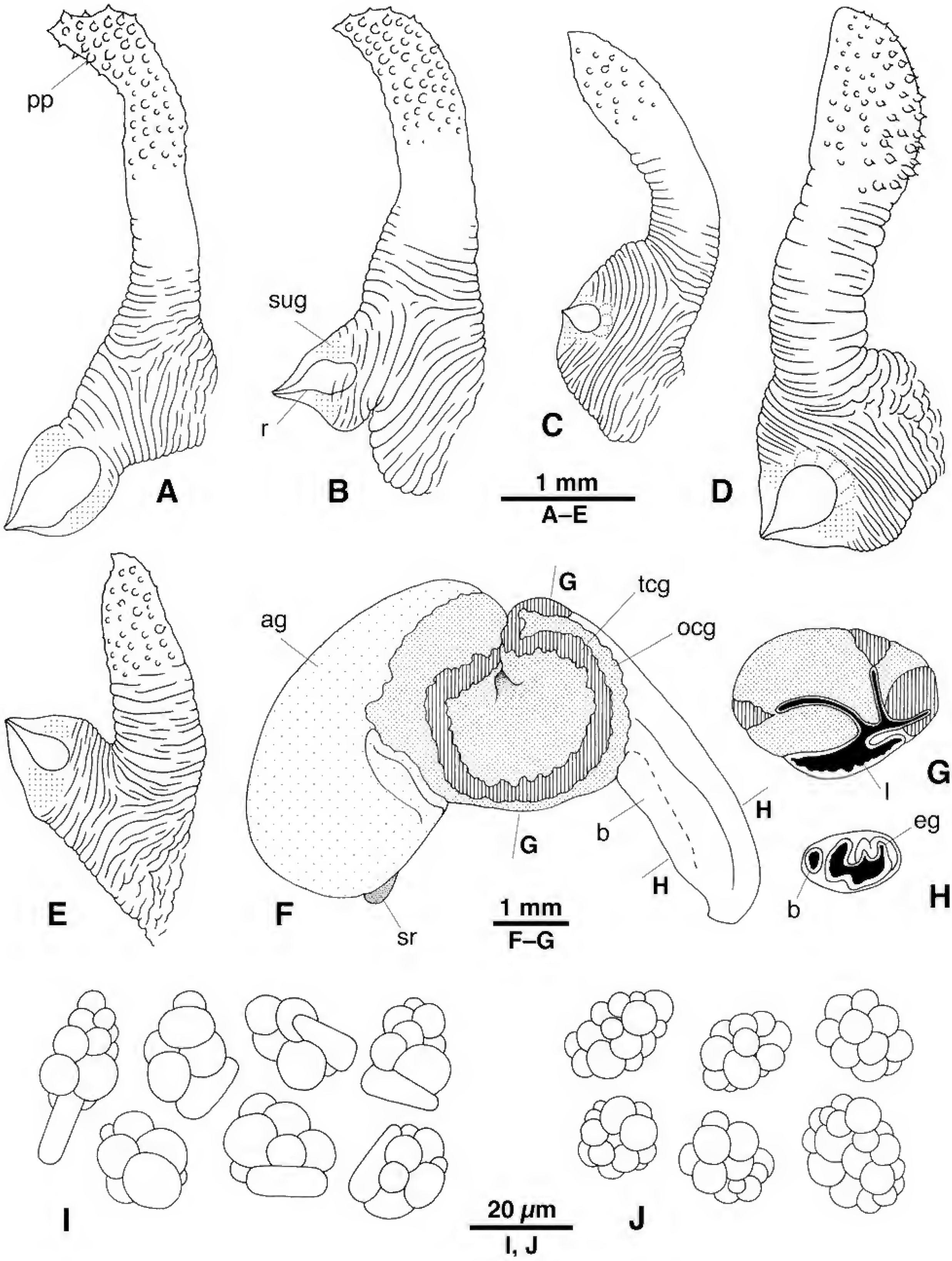

Fig. 3. *Nodilittorina pyramidalis*: (*A–E*) Penes. (*F*) Pallial oviduct with transverse sections (*G,H*). (*I,J*) Paraspermatozoa from two specimens. (*A,B*) Mollymook, NSW, Australia (BMNH 20030390). (*C*) Fairlight, Sydney, NSW, Australia (BMNH 20030391). (*E,I,J*) North Harbour, Sydney, NSW, Australia (BMNH 20030392). (*F–H*) Mullimburra Point, NSW, Australia (AMS C356720). Shell heights: (*A*) 12.0 mm; (*B*) 11.1 mm; (*C*) 10.3 mm; (*D*) 15.0 mm; (*E*) 12.0 mm; (*F*) 17.0 mm. Abbreviations: (*ag*) albumen gland; (*b*) copulatory bursa (visible by transparency); (*eg*) egg groove; (*ocg*) opaque capsule gland; (*pp*) penial papillae; (*r*) receptacle of mamilliform penial gland (visible by transparency); (*sr*) seminal receptacle; (*sug*) subepithelial glandular tissue (visible by transparency, not a discrete penial glandular disc); (*tcg*) translucent capsule gland.

capsule sculptured with spiral ridges; penis variable, but often with single mamilliform gland and glandular disc. This definition greatly increased the number of species, because it included the smooth, striate forms formerly classified as *Littorina (Austrolittorina)*. It was essentially supported, with some modifications, by new anatomical information on paraspermatozoa and pallial oviducts (Reid, 1986, 1989). This broad definition has persisted in the taxonomic literature (Reid, 2001, 2002*a*) and the most recent review listed 60 species of *Nodilittorina* (Reid, 2002*b*).

However, a rigorous phylogenetic definition of the genus has proved elusive, suggesting that this large group is not a monophyletic one. The first attempt at a parsimony analysis of morphological characters of the Littorinidae included four exemplars of *Nodilittorina*, and only a single, non-unique synapomorphy was discovered for the genus, the banding pattern of the cephalic tentacles (Reid, 1989). A recent analysis of the morphological characters of all 60 species then included in *Nodilittorina* produced a poorly resolved tree, in which all but two *Nodilittorina* species formed a paraphyletic group within a clade that also included the genus *Littorina sensu stricto* (Reid, 2002*b*). This *Nodilittorina* plus *Littorina* clade was defined by the one unique and unequivocal synapomorphy of the form of the outer marginal radular teeth (with a flange on either side of the base), although this character state was reconstructed as lost within *Littorina*. According to this interpretation, all other features previously used to characterize *Nodilittorina* were plesiomorphic similarities and without phylogenetic significance. Analysis of DNA sequence data has now shown unequivocally that *Nodilittorina* in the broad sense is not a monophyletic group, and has supported the integrity of three distinct clades: a large clade of 50 tropical species (for which the name *Echinolittorina* is available), a clade of five species from Australia, New Zealand and South America (a restricted use of Rosewater's genus *Austrolittorina*), and a clade of four species from southern Africa and Australia (for which the new name *Afrolittorina* was established) (Williams *et al.*, 2003). There was no strong support for the inclusion of the remaining species, *Nodilittorina pyramidalis*, in these or other generic-level clades. This is the type species of the genus (Abbott, 1954) and it is therefore appropriate to treat *Nodilittorina* as monotypic.

From the perspective of stability of taxonomic usage of the generic name *Nodilittorina*, the identity of its type species is unfortunate. The designation of *N. pyramidalis* as the type species has a confused history. Under his original description of *Littorina (Nodilittorina)* von Martens (1897) listed the names *nodulosa* Pfeiffer, *dilatata* d'Orbigny, *trochiformis* Dillwyn, *antonii* Philippi and *granosa* Philippi, he gave a detailed description of *L. vilis* Menke, and gave notes on *L. pyramidalis* Quoy & Gaimard, *L. natalensis* Krauss in Philippi and *L. subnodosa* Philippi. The first designation of a type species was by Wenz (1938) who, without discussion, gave the type as "*T. (N.) nodulosus* (Gmelin) [*Turbo*]". Abbott (1954) rejected this designation as invalid, on the grounds that *Turbo nodulosus* Gmelin, 1791 was not among the species included by von Martens (1897) and because it is a turbinid species. (In fact it is an *Angaria*; the littorinid species that Wenz presumably intended was *Trochus nodulosus* Gmelin, 1791.) Abbott (1954, following Clench & Abbott, 1942) interpreted "*nodulosa* Pfeiffer", as listed by von Martens (1897), as the species now classified as *Tectarius (Tectininus) antonii* (Philippi, 1846), whereas he believed *Trochus nodulosus* Gmelin to be based on both *N. dilatata* and *N. pyramidalis*. However, as pointed out by Kadolsky (1971; Bandel & Kadolsky, 1982), Pfeiffer was not in fact the author of the name *nodulosa* as listed by von Martens (1897), but only of the new combination *Litorina nodulosa* (Gmelin). A case might therefore be made that Wenz's (1938) designation was valid, although this could be dismissed on the technicality of his mistaken use of the original genus *Turbo*. Gmelin's species *Trochus nodulosus* is based on figures by Chemnitz (1781) that are here interpreted to represent the species currently classified as *Echinolittorina trochoides* (Gray, 1839) (see Taxonomic History of *N. pyramidalis* below). Rejecting Wenz's designation of this species, Abbott (1954) instead proposed *Littorina pyramidalis* as the type of *Nodilittorina*. Abbott himself believed this to be the earliest valid name for a species that included the two taxa now recognized as *N. pyramidalis* and *E. trochoides* (*Trochus nodulosus* Gmelin is unavailable, as it is a junior homonym of *T. nodulosus* Solander, 1766). He therefore probably aimed to fulfil the intention of Wenz. Although to allow Wenz's (1938) designation would preserve *Nodilittorina* more nearly in its accustomed usage, it seems preferable to accept the designation by Abbott (1954). This avoids the doubt surrounding the identity of Gmelin's species. Furthermore, *N. pyramidalis* has been accepted as the type species for nearly 50 years, even if it has been frequently misidentified during that time.

Further details of the history of the usage of *Nodilittorina*, including subgeneric divisions and inclusion of species now assigned to other genera, are available elsewhere (Reid & Geller, 1997; Reid, 2002*a*,*b*).

Diagnosis. Shell nodulose; nodules not axially aligned; eroded parietal area; no pseudoumbilicus; unpatterned. Cephalic tentacles with 2 broad black longitudinal stripes. Penis with swollen filament bearing numerous minute papillae; base bifurcate; single mamilliform gland surrounded by subepithelial glandular tissue (not separated as distinct glandular disc or flap); penial vas deferens an open groove. Paraspermatozoa with small rod bodies. In pallial oviduct egg groove makes a simple loop through albumen gland, circular loop through capsule gland, no loop in jelly gland; copulatory bursa opens in anterior position near anterior end of pallial oviduct. (After Williams *et al.*, 2003.)

Nodilittorina pyramidalis (Quoy & Gaimard, 1833)

Figs. 2–3, 4A,B, 5

Littorina pyramidalis Quoy & Gaimard, 1833: 482–483, pl. 33, figs. 12–13, figs. 14–15 (tentacles and foot) (Baie Jervis, Nouvelle-Hollande [Jervis Bay, New South Wales, Australia]; lectotype (Rosewater, 1970) (fig. 2G), 1 dry paralectotype, 2 paralectotypes in alcohol, MNHNP, seen). Deshayes, 1843: 210. Reeve, 1857: *Littorina* sp. 14, pl. 2, fig. 14. Tenison Woods, 1879: 69–71.

Litorina pyramidalis.—Philippi, 1846:143, *Litorina* pl. 2, figs. 10, 12.

Tectarius pyramidalis.—Adams & Adams, 1854: 315. Angas, 1867: 209. Hedley, 1918: M51.

Littorina (Tectus) pyramidalis.—Nevill, 1885: 156.

Littorina (Nodilittorina) pyramidalis.—von Martens, 1897: 205.

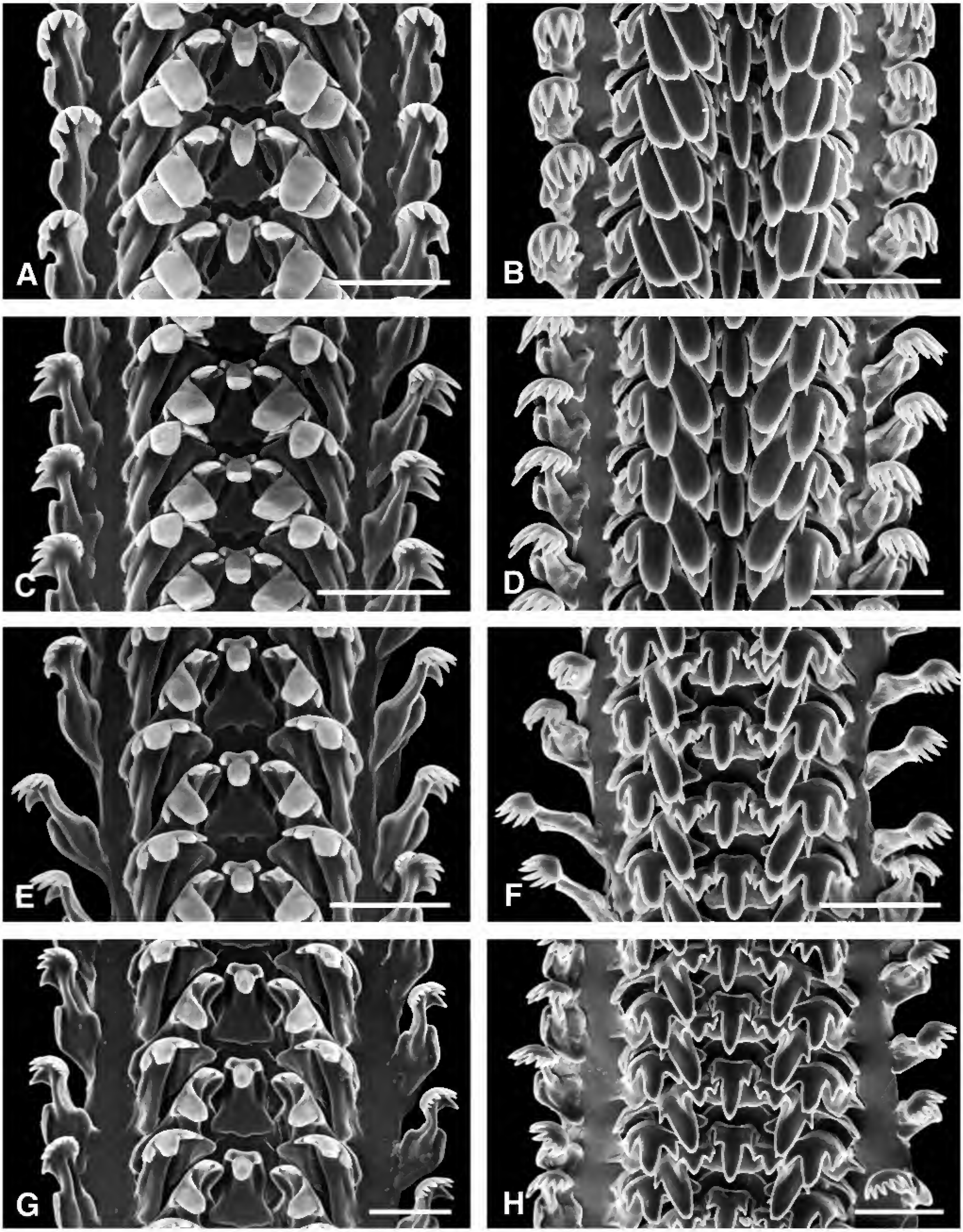

Fig. 4. Radulae; views of same specimen flat (*A,C,E,G*) and at 45° from anterior end (*B,D,F,H*). (*A,B*) *Nodilittorina pyramidalis*, Mollymook, NSW, Australia (BMNH 20030390; shell H = 14.6 mm). (*C,D*) *Austrolittorina unifasciata*, Mollymook, NSW, Australia (BMNH 20030393; shell H = 10.5 mm). (*E,F*) *Austrolittorina antipodum*, Wellington Harbour, New Zealand (BMNH 20030394; shell H = 8.8 mm). (*G,H*) *Austrolittorina cincta*, Bethels Beach, Auckland, New Zealand (BMNH 20030395; shell H = 12.0 mm). Scale bars = 50 µm.

Nodilittorina pyramidalis.—Abbott, 1954: 451, 456 (in part; includes *Echinolittorina trochoides*). McMichael, 1959: 27. Iredale & McMichael, 1962: 38. Macpherson & Gabriel, 1962: 90, fig. 119 (in part; includes *E. trochoides*). Wilson & Gillett, 1971: 30 (in part; pl. 11, fig. 11, 11a are *E. trochoides*). Wilson & Gillett, 1979: 52 (in part; pl. 8, fig. 3 is *E. trochoides*; pl. 8, fig. 3a is *E. australis* [Gray, 1826]). Jansen, 1995: 31, fig. 95; Reid, 1998: 739, fig. 15.100B, E (oviduct). Reid, 2002*b*: figs. 1A, 2B (penis). Williams *et al*., 2003.

Nodilittorina (Nodilittorina) pyramidalis pyramidalis.—Rosewater, 1970: 424, 481–484, pl. 325, figs. 24, 25, pl. 370, figs. 1, 2, 6, 7, pl. 372 (distribution) (in part; other figures are *E. trochoides*).

Nodilittorina (Nodilittorina) pyramidalis.—Reid, 1989: 100, pl. 2, fig. 2i, figs. 7k (penis), 10j (oviduct), 14l (radula). Wilson, 1993: 147 (in part; pl. 18, fig. 5a,b are *E. trochoides*).

Litorina (Tectarius) nodulosa.—Weinkauff, 1882: 43–44, pl. 5, figs. 5–6 (not *Trochus nodulosus* Gmelin, 1791 = *E. trochoides*). Weinkauff, 1883: 225 (as *Tectaria*; not Gmelin, 1791).

Tectarius nodulosus.—Tryon, 1887: 258, pl. 48, fig. 72 (not Gmelin, 1791; in part; includes *Echinolittorina tuberculata, E. trochoides, Tectarius antonii*).

Littorina nodulosa.—Etheridge, 1889: 24 (not Gmelin, 1791).

Tectaria nodulosa.—Tate & May, 1901: 389 (not Gmelin, 1791).

Nodilittorina nodulosa.—Fischer, 1967: 47–80 (not Gmelin, 1791; in part; includes *E. trochoides*). Fischer, 1969: 119–129 (not Gmelin, 1791; in part; includes *E. trochoides*).

Tectarius tuberculatus.—Iredale, 1924: 243–244 (not *Litorina tuberculata* Menke, 1828 = *Echinolittorina tuberculata*).

Nodilittorina tuberculata.—Allan, 1950: 80, textfig. 19: 7 (not Menke, 1828). Macpherson & Chapple, 1951: 118 (not Menke, 1828).

Taxonomic history. This species has a complex taxonomic history, as a result of the longstanding confusion of at least six littorinid species that have superficially similar nodulose shells. Gmelin (1791) based his *Trochus nodulosus* on two figures in Chemnitz (1781: pl. 163, figs. 1545, 1546) of shells obtained by Captain Cook in the South Seas. These have been interpreted as examples of the present species (Weinkauff, 1882), which does indeed occur at Cook's landing place in Botany Bay (Iredale, 1924). However, if the figure is an accurate representation, the tall spire with small white nodules, nodulose base, narrow columella and rounded anterior lip, together leave little doubt that the species is that now identified as *Echinolittorina trochoides* (see Remarks below), which could well have been obtained during Cook's itinerary further north in Australia. Most subsequent authors failed to discriminate between *N. pyramidalis*, endemic to southeastern Australia, and *E. trochoides*, widespread in Indo-Malaya, and used the same name for both. Following Weinkauff (1882), some adopted the name *nodulosa* (e.g., Tryon, 1887; Fischer, 1967), overlooking the fact that it was unavailable, being a junior primary homonym of *Trochus nodulosus* Solander, 1766. Iredale (1924) believed that the earliest available name was *Litorina tuberculata* Menke, 1828, but this is a western Atlantic species (included by Gmelin as variety "minor" of his *T. nodulosus*; see discussion by Abbott, 1954; Bandel & Kadolsky, 1982). The first available name for a nodulose, western Pacific species is *Littorina pyramidalis* Quoy & Gaimard, 1833 and this has been widely used in the literature.

At first, the epithet *pyramidalis* was correctly applied, to include only the present species (Philippi, 1846; Reeve, 1857; Angas, 1867; Nevill, 1885; von Martens, 1897), but from the end of the nineteenth century a broader species concept began to prevail. Tryon (1887) considered that nodulose shells from the western Atlantic and western Pacific were indistinguishable and synonymized them as *Tectarius nodulosus*. Abbott (1954) used the name *Nodilittorina pyramidalis* for a supposed single species extending from India to Australia and the Far East (i.e. *N. pyramidalis* s.st. and *E. trochoides*). A similar concept was adopted by Fischer (1967, as *N. nodulosa*) and by Rosewater (1970, but with an additional subspecies *N. pyramidalis pascua* Rosewater, 1970, on Easter Island, now regarded as a distinct species of *Echinolittorina*). It is in this incorrect sense that the name *N. pyramidalis* has since been generally applied. Meanwhile, some Australian workers had correctly observed that two nodulose species occurred in eastern Australia. This was presumably the basis for the inclusion of both *Tectarius malaccanus* (Philippi, 1847) (= *E. trochoides*) and *T. nodulosus* (presumably *N. pyramidalis*) in Hedley's (1910) list of Queensland shells. Iredale & Allan (1940) and Endean *et al*. (1956) also remarked on the likely presence of two *Nodilittorina* species in eastern Australia, but without making any taxonomic recommendation. Nevertheless, it was only in 1989 that both *N. pyramidalis* and *N. trochoides* appeared in the list of worldwide Littorinidae (Reid,1989; updated by Reid, 2002*b*) and the latter was formally redescribed by Reid (1992, 2002*a*). Although some of its characters have been illustrated in phylogenetic studies (Reid, 1986, 1989, 2002*b*; also Reid, 1998), the present account is the first full description of *N. pyramidalis*.

From the original figure, without locality or details, *Littorina duplicata* Deshayes, 1850 appears superficially similar to *N. pyramidalis*; however, it is a fossil species probably belonging to the family Amberleyidae (based on examination of non-type specimens labelled *Littorina duplicata* in MNHNP).

Diagnosis. Shell large; two rows of prominent nodules on last whorl, nodules not axially aligned, no nodules on base; blue-grey; aperture brown with two cream bands. Penis with numerous minute mamilliform glands in swollen filament; single large mamilliform gland on base, but no distinct glandular disc. Pallial oviduct with two consecutive loops of egg groove, in albumen and capsule glands; copulatory bursa opens near anterior end of pallial oviduct.

Material examined. 94 lots (56 AMS, 9 USNM, 24 BMNH, 2 IRSNB, 2 ZMA, 1 NMW), including 18 penes, 4 sperm samples, 6 pallial oviducts, 3 radulae.

Shell (Fig. 2). Mature shell height 8.6–26.8 mm. Shape high-turbinate to conical (H/B = 1.23–1.46; SH = 1.59–2.02); shoulder of spire whorls with single row of pointed nodules; single row of nodules on shoulder and another at periphery of final whorl; moderately solid. Columella short, broad, excavated, slightly flared or projecting as a rounded lip anteriorly; eroded parietal area present. Sculpture of fine raised spiral threads over entire surface, 19–25 on final whorl, separated by grooves equal in width to threads, threads weaker towards centre of base; spiral microstriae cover surface, but are frequently eroded; two rows of prominent pointed nodules at shoulder and periphery of final whorl, each 12–25, but not strictly aligned along axial (prosocline) growth lines; axial growth lines prominent, closely spaced, becoming lamellose towards end of final whorl, with no consistent relation to nodules. Protoconch not well preserved, but about 0.4 mm diameter and about 3 whorls. Colour blue-grey, darker where eroded, with whitish nodules; aperture dark brown with two cream bands (corresponding with base and shoulder of whorl).

Animal. Head and sides of foot grey to black; tentacle with two broad (sometimes indistinct) black stripes, sometimes fused to become almost entirely black, pale at tip. Opercular ratio 0.54–0.63. Penis (Fig. 3A–E): filament relatively short, 0.3–0.5 total length of penis, slightly pointed and usually swollen, sometimes reddish, no constriction differentiating filament from wrinkled base, filament bears numerous papillae (structurally, these are miniature mamilliform penial glands, with mucous reservoir and subepithelial glandular tissue; Reid, 1989); sperm groove open to tip; single large mamilliform gland in short lateral projection of base, surrounded by subepithelial glandular tissue homologous with penial glandular disc (but not separated as a distinct glandular flap, and sometimes only visible by histology); penis unpigmented; penis reduced in size from April to June, but not shed (Underwood, 1974). Euspermatozoa 117–123 µm; paraspermatozoa (Fig. 3I,J) are clusters of large spherical granules, 15–25 µm diameter, sometimes with short wedge-shaped or elongate rod bodies visible. Pallial oviduct (Fig. 3F–H) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, opaque pink, within which portion adjacent to egg groove (translucent capsule gland) is differentiated as a ring, reddish when fresh; copulatory bursa confined to straight section of pallial oviduct, opening near anterior end.

Spawn and development. Not recorded, but protoconch and large capsule gland indicate pelagic spawn and planktotrophic development; from condition of ovary, spawning at a maximum in January and February (Underwood, 1974).

Radula (Fig. 4A,B). Relative radular length 2.3–4.0. Rachidian: length/width 1.25–1.80; major cusp elongate, rounded or pointed at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded at tip. Outer marginal: 6–7 cusps.

Habitat. This species is common in the littoral fringe of rocky shores; it is the dominant mollusc above high water of spring tides, extending higher where splash and spray permit (Endean *et al.*, 1956) and exceptionally up to 12 m above sea level (Dakin *et al.*, 1948). It thus extends to higher levels than the sympatric *Austrolittorina unifasciata*, and occurs at lower densities (to 32 m^{-2} at Cape Banks, NSW; Branch & Branch, 1981). It occurs mainly on ocean coasts and is said to be more common on shores of moderate to high exposure to waves (Endean *et al.*, 1956), although it can sometimes be found on moderately sheltered shores in inlets and harbours. Quantitative study has failed to find a consistent correlation between density and wave exposure near Sydney (Chapman, 1995a). On a small scale, the highest densities are associated with microhabitats of deep crevices, cracks and pits, whereas few occur on open rock surfaces (Chapman, 1994b). Although largely restricted to the top of the shore, animals occur sporadically on the upper mid-shore, where pits and topographic irregularities allow (Chapman, 1994b). Small specimens have been reported lower on the shore than adults (Johnston, 1917) and are scarce, so that recruitment appears sparse and probably occurs mainly within pits in the rock (Underwood, 1974; Chapman, 1994b; Chapman & Underwood, 1994). Dispersion and behaviour have been studied (Chapman & Underwood, 1994; Chapman, 1999).

Range (Fig. 5). Eastern Australia, from easternmost Victoria to southern Queensland; Lord Howe Island and Norfolk Island. The only record from Victoria is from Mallacoota (37°33'S 149°47'E, AMS C50368; Bennett & Pope, 1953; Macpherson & Gabriel, 1962). The species is abundant along the entire length of the rocky coastline of New South Wales, and is also frequent in southern Queensland as far north as Noosa Heads (26°23'S 153°09'E, AMS C386700). Further north *N. pyramidalis* has been recorded from only four localities: Urangan, Hervey Bay (25°17'S 152°54'E, AMS C386710), Bustard Bay (24°05'S 151°48'E, AMS C62608), North Keppel Island (23°04'S 150°54'E, AMS C386762 plus 3 more lots) and Ocean Heads, Yeppoon (23°8.5'S 150°46'E, AMS C386768 plus 2 more lots). This species occurs at Lord Howe Island (AMS C089673; BMNH 1925.5.7.1; USNM 684715; Iredale & Allan, 1940), but is said to be "not common" (Etheridge, 1889, as *Littorina nodulosa*). There is a single old record from Norfolk Island (AMS C059382, A. Bell, 1910–1911).

Remarks. The shell does not show conspicuous variation (Fig. 2). Statistically, there are significant differences in shape between shores, but this is not correlated with wave exposure, overall size or population density (Chapman, 1995a). On one pair of shores at Cape Banks the shell aperture and foot were larger on the wave-exposed shore than on the more sheltered one, but it is not known if this is a general pattern (Chapman, 1997).

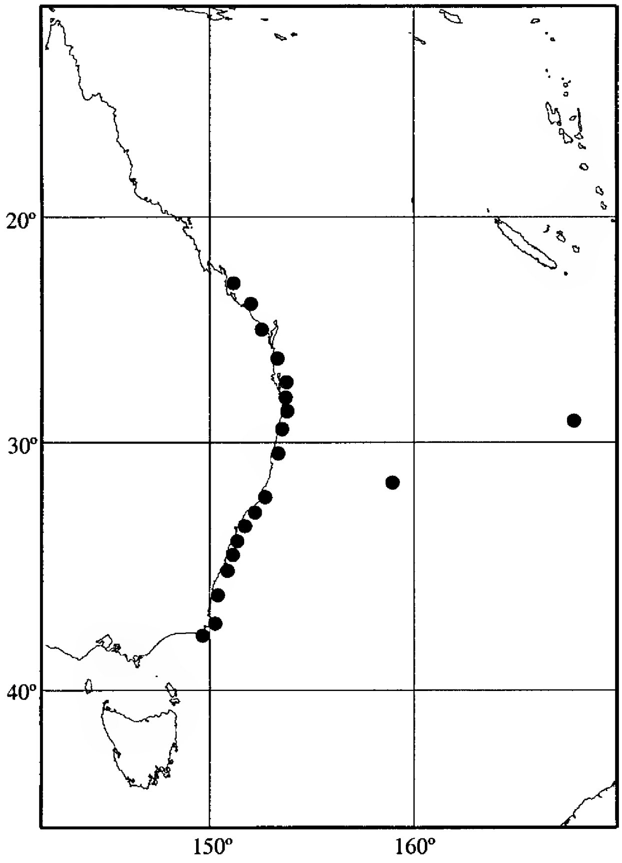

Fig. 5. Distribution of *Nodilittorina pyamidalis*.

Table 2. Characters useful for the discrimination of *Nodilittorina pyramidalis* and *Echinolittorina trochoides*.

character	*Nodilittorina pyramidalis*	*Echinolittorina trochoides*
geographical range	Yeppoon, Queensland to Mallacoota, Victoria	tropical Australia south to Hervey Bay; elsewhere Indo-Malaya to Japan
shell		
height	8–27 mm	6–18 mm
shape	broader (H/B 1.23–1.46)	narrower (H/B = 1.49–1.72)
nodules	1 row of nodules on penultimate whorl	usually 2 rows of nodules on penultimate whorl
basal sculpture	cords not nodulose	cords usually bear small nodules
apertural shape	slightly flared and angled at base of columella	anterior edge more rounded
colour	blue-grey with white nodules	grey-brown with cream nodules
apertural colour	brown with 2 cream bands	brown with single basal cream band
penis		
filament	many papillae (minute mamilliform glands) on swollen filament	no papillae on smoothly tapering filament
base	no discrete glandular disc adjacent to large mamilliform gland	glandular disc adjacent to large mamilliform gland
pallial oviduct		
egg groove	egg groove makes large circular loop in capsule gland	no loop in capsule gland
copulatory bursa	simple sac	bursa divides into two branches

The distributions of *N. pyramidalis* and the conchologically similar *Echinolittorina trochoides* are almost mutually exclusive in eastern Australia. The former is characteristic of the eastern overlap zone (Ponder & Wells, 1998), whereas the latter is a widespread tropical species. Based on a survey of the distribution of common intertidal organisms along the Queensland coast, Endean *et al*. (1956) placed the biogeographic boundary between shores of northern (tropical) and southern (temperate) character at 25°S (Hervey Bay). This is also the southernmost record of *E. trochoides* (AMS C386753, Point Vernon, Hervey Bay, 25°15'S 152°49'E). These two species have been recorded together at only two localities: Bustard Bay (24°05'S 151°48'E; although in two separate lots: *N. pyamidalis* AMS C62608; *E. trochoides* AMS C386794) and the Keppel Islands (23°04'S 150°54'E; three formerly mixed lots of the two species in AMS now separated and registered as: C106933 plus 386781, C089660 plus 386787, C386762 plus 386780, numbers of *N. pyramidalis* plus *E. tochoides* in these lots are: 31 plus 2, 60 plus 1, 54 plus 33, respectively). Endean *et al*. (1956) pointed out that this faunistic boundary was not correlated with temperature change and suggested that exposure to wave action was critical. South of 25°S the coast is exposed to strong surf and oceanic swells, whereas to the north it is largely sheltered by the Great Barrier Reef. Presumably other hydrographic factors, such as nutrients and productivity, are also connected with the contrast between oceanic and reef-sheltered coasts. The distribution of *N. pyramidalis* and *E. trochoides* north of 25°S does correlate to some extent with wave-exposure. Bustard Bay (where both have been recorded) is semi-exposed (Endean *et al*., 1956), whereas in the shelter of nearby Port Curtis only *E. trochoides* has been found. Yeppoon (and presumably the adjacent Keppel Islands) is an exposed locality (Endean *et al*., 1956). Nevertheless, in the southern parts of its range *E. trochoides* does occur in both exposed and sheltered localities. The seven collections of *N. pyramidalis* from Yeppoon and the Keppel Islands in AMS are not all precisely dated, but five are pre-1950 and two no later than 1966; it is not known whether this species can still be found there.

The discrimination of *N. pyramidalis* and *E. trochoides* is usually straightforward (Table 2). Their geographical ranges barely overlap and anatomical features are diagnostic. In females, the loop of the egg groove through the capsule gland is present only in *N. pyramidalis*, whereas a forked copulatory bursa is unique to *E. trochoides* (Reid, 1992: fig. 2i) In males, papillae on the penial filament and lack of a discrete glandular disc distinguish *N. pyramidalis* (cf. *E. trochoides*, Reid, 1992: fig. 1j; Reid, 2002*b*: fig. 2E). The larger, broader shell and produced anterior lip of *N. pyramidalis* are the most useful conchological characters, but small shells can be difficult to separate. In the northern parts of its range the shells of *N. pyramidalis* are smaller; those from Queensland rarely exceed 18 mm and in the three sympatric samples of *N. pyramidalis* and *E. trochoides* the largest of the 145 specimens of *N. pyramidalis* is only 14.8 mm. In these mixed samples the two species are mainly of similar size and separation requires careful examination of aperture shape, coloration and sculpture (Table 2; for *E. trochoides* see Reid, 1992: pl. 3a–c; Reid, 2001: fig. 2G, H). The largest shells of *N. pyramidalis* are found on Lord Howe Island, where sizes of greater than 23 mm are common.

The phylogenetic relationships of *Nodilittorina pyramidalis* remain unclear. In a recent analysis of DNA-sequence data from two nuclear and two mitochondrial genes, Williams *et al*. (2003) showed only that it was a member of a large clade including the genera *Tectarius*, *Austrolittorina, Cenchritis* and *Littoraria*. Within this group, the most likely (but still weakly supported) positions were at the base of the clade, or as the sister-group of *Tectarius*. This latter possibility is intriguing, for it is supported by the unique feature of papillae on the penial filament, shared by *N. pyramidalis* and the subgenera *Tectarius, Tectininus* and *Echininus* of *Tectarius* (but not the subgenera *Liralittorina* or *Echininiopsis*). Other features such as the form of the outer marginal radular teeth and the loop of the egg groove within the capsule gland, which had been interpreted as evidence for a relationship with *Austrolittorina* (Reid, 2002*b*) are now known to be convergent (Williams *et al*., 2003).

Austrolittorina Rosewater, 1970

Littorina (Austrolittorina) Rosewater, 1970: 467 (type *Littorina unifasciata* Gray, 1826, by original designation).

Taxonomic history. This generic name was introduced as a subgenus of *Littorina* (implicitly by reason of the smooth, spirally striate shell of its members, see Taxonomic History of *Nodilittorina*, above). In the original diagnosis, Rosewater (1970) mentioned a "predominantly southern ocean and tropical distribution", "flattened columella and crescent-shaped area on the adjacent part of the shell" (i.e. the eroded parietal area), and a penis with single penial gland and penial glandular disc (in terminology of Reid, 1989; i.e. penis of the type characteristic of *Nodilittorina s.l.*). No unique features were identified by which to define the group and, in addition to the species here included, at least nine others (belonging to *Echinolittorina, Afrolittorina* and *Littoraria* in current classification) were listed. Three further species were added subsequently (Ponder & Rosewater, 1979). As discussed above, with new insights into the anatomy of littorinids the definition of *Nodilittorina* was broadened and *Austrolittorina* placed in its synonymy (Bandel & Kadolsky, 1982; Reid, 1989). The name was not used again until Reid (2002*a*) provisionally employed it as a subgenus of *Nodilittorina*, to denote eight or nine Southern Ocean species united by a loop of the egg groove within the capsule gland of the pallial oviduct (*N. araucana* was not then recognized as belonging to this group). Formal phylogenetic analysis of the morphological characters of *Nodilittorina s.l.* failed to confirm these ten southern species as a clade, and as a result no taxonomic decisions were made (Reid, 2002*b*).

In a recent molecular study, all ten of these southern littorinines were included and the five species here included in *Austrolittorina* appeared as a strongly supported clade; the name was therefore used at the rank of genus for the first time, and a formal diagnosis given (Williams *et al*., 2003). Of the morphological characters listed in the following diagnosis, none is unique. One that is, however, distinctive is the absence of axial colour markings (i.e. axial lines, or axially aligned series of spots or dashes) that characterize the majority of littorinine species. Shells are not always of the bluish-white appearance of the type species, *A. unifasciata*; *A. araucana* may be brown or whitish and *A. cincta* typically has spiral brown lines.

Diagnosis. Shell not nodulose; spiral striae or smooth; eroded parietal area; no pseudoumbilicus; white with peripheral blue-grey band, brown, or with spiral brown lines; no axial colour pattern. Cephalic tentacles black. Penis with swollen filament; base bifurcate; single mamilliform gland adjacent to glandular disc of subepithelial glandular tissue; penial vas deferens an open groove. Paraspermatozoa with short, curved or coiled rod bodies, or rod bodies absent. In pallial oviduct egg groove makes a simple loop through albumen gland, circular loop (or only slight flexure) through capsule gland, no loop in jelly gland; copulatory bursa opens in anterior or posterior position. (After Williams *et al*., 2003.)

Austrolittorina unifasciata (Gray, 1826)

Figs. 4C,D, 6–8, 25A,B

Littorina unifasciata Gray, 1826: 483 (Australia; restricted to King George Sound, Western Australia (Rosewater, 1970); lectotype (Rosewater, 1970) BMNH 1968373/1 (fig. 6A) plus 1 paralectotype BMNH 1968373/2, seen). Angas, 1865: 172. Tenison Woods, 1878: 36. Guiler, 1958: 139. Haacke, 1885: 504–505 (in part, includes *Afrolittorina praetermissa*). Wilson & Gillett, 1979: 52, pl. 8, fig. 6, 6a.

Litorina unifasciata.—Menke, 1844: 57.

Melarhaphe unifasciata.—Iredale, 1915: 447 (in part; includes *A. antipodum*). Hedley, 1916: 186 (as *Melaraphe*). Hedley, 1918: M51. May, 1921: 48. May, 1923: 49, pl. 22, fig. 19. Cotton & Godfrey, 1938: 10. Macpherson & Chapple, 1951: 118 (as *Melaraphe*). Kershaw, 1955: 307 (as *Melaraphe*). Wilson & Gillett, 1971: 30, pl. 11, fig. 12, 12a (as *Melaraphe*).

Melarapha unifasciata.—McMichael, 1959: 27. Macpherson & Gabriel, 1962: 87, fig. 115.

Littorina (Austrolittorina) unifasciata unifasciata.—Rosewater, 1970: 423, 467–470, pl. 325, figs. 17–18, 326, fig. 5, pl. 359, figs. 1–5, pl. 360, figs. 1–4, pl. 361, figs. A (radula), C (penis), pl. 362 (distribution).

Nodilittorina (Nodilittorina) unifasciata unifasciata.—Bandel & Kadolsky, 1982: 37.

Littorina (Austrolittorina) unifasciata.—Ludbrook & Gowlett-Holmes, 1989: 564, fig. 11.19j, k. Wilson, 1993: 146–147, pl. 18, fig. 3.

Nodilittorina (Nodilittorina) unifasciata.—Reid, 1989: 100, pl. 2, fig. 2j.

Nodilittorina unifasciata.—Jansen, 1995: 31, fig. 94. Reid, 1998: 739, fig. 15.100D (penis). Reid, 2002*b*: fig. 1c.

Nodilittorina (Austrolittorina) unifasciata.—Reid, 2002*a*: 154.

Austrolittorina unifasciata.—Williams *et al*., 2003.

Littorina diemenensis Quoy & Gaimard, 1833: 479–480; pl. 33, figs. 8–10 (la partie sud de la Nouvelle-Hollande, de l'île de Van-Diémen et même de la Nouvelle-Zélande [southern Australia, Tasmania and New Zealand]; restricted to Tasmania (Rosewater, 1970); lectotype (Rosewater, 1970) MNHNP 10.2×5.9 mm plus 11 dry paralectotypes plus 11 dry paralectotypes plus 82 alcohol paralectotypes plus 39 alcohol paralectotypes, all MNHNP, seen; in part; from locality New Zealand, includes *L. antipodum*). Deshayes, 1843: 209. Reeve, 1858: *Littorina* sp. 94, pl. 17, fig. 94. Nevill, 1885: 141.

Littorina (Melarhaphe) diemenensis.—Adams & Adams, 1854: 314 (as *Melaraphe*).

Melarapha diemenensis.—Iredale & McMichael, 1962: 38.

Litorina acuta Menke, 1843: 9 (Western Australia; types presumed lost; synonymized with *Littorina unifasciata* Gray, 1826, by Menke, 1844).

Litorina mauritiana.—Philippi, 1847: 165; *Litorina* pl. 3, fig. 17a (not *Phasianella mauritiana* Lamarck, 1822 = *Littoraria mauritiana*; in part; figs. 15 and 17b are *Echinolittorina ziczac* (Gmelin, 1791), also includes *Littoraria mauritiana*). Weinkauff, 1882: 97–98 (not Lamarck, 1822; pl. 14, fig. 4 is *E. ziczac*; also includes *L. mauritiana*). Weinkauff, 1883: 220 (not Lamarck, 1882; in part; includes *L. mauritiana*). Watson, 1886: 574 (not Lamarck, 1822; in part; includes *L. mauritiana*). Verco, 1908: 8 (not Lamarck, 1822). Hedley, 1910: 355.

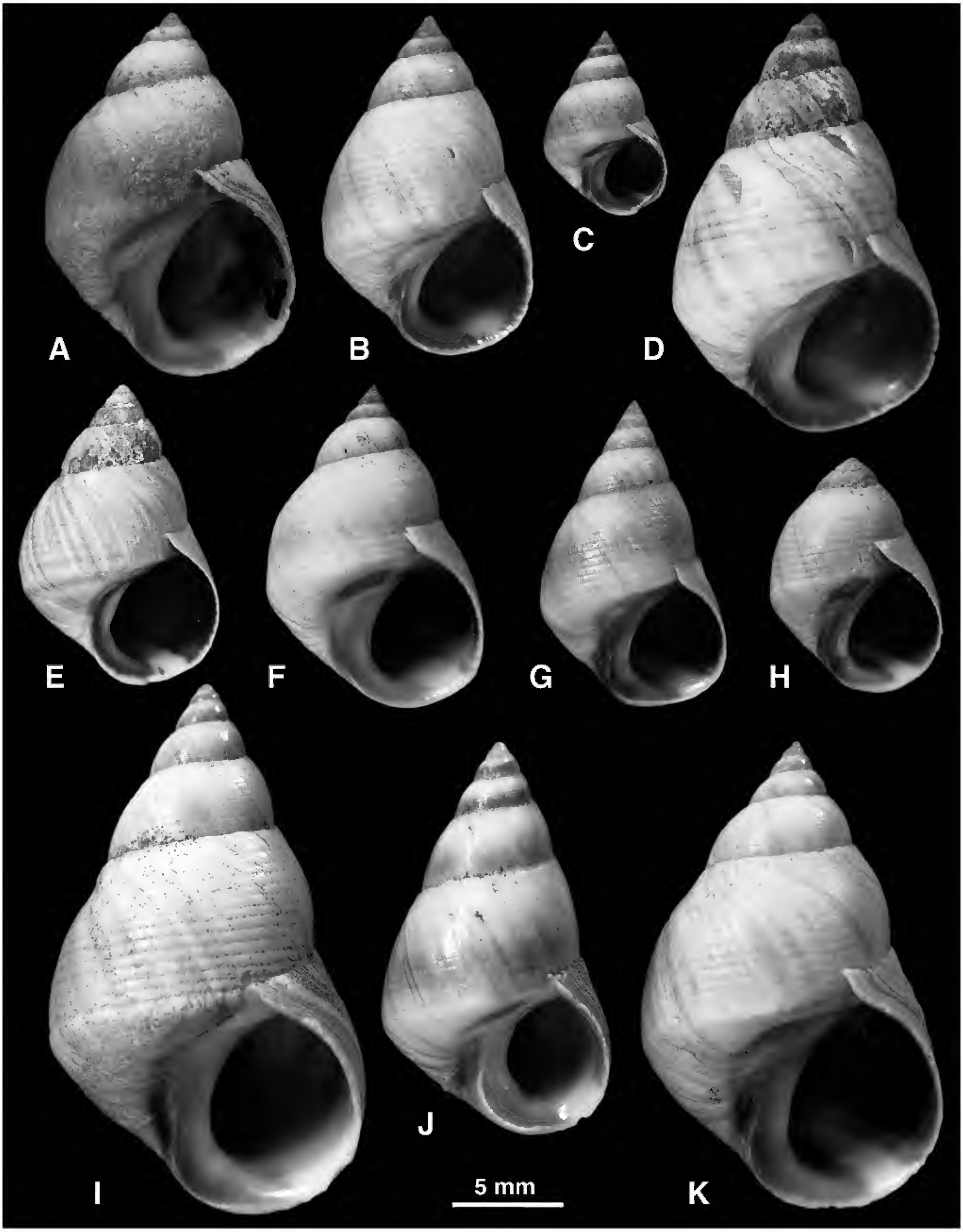

Fig. 6. *Austrolittorina unifasciata*: (*A*), lectotype of *Littorina unifasciata* Gray, 1826; no locality (BMNH 1968373/1). (*B,D*) Mollymook, NSW, Australia (BMNH 20030396). (*C*) Stony Point, Western Port Bay, Victoria, Australia (BMNH 20030397). (*E*) Fairlight, Sydney, NSW, Australia (BMNH 20030398). (*F,G*) Trigg Island, WA, Australia (BMNH 20030399). (*H*) Bucroft Head, Jervis Bay, NSW, Australia (BMNH 1925.4.1.16). (*I–K*) Lord Howe Island (AMS C059516).

Littorina mauritiana.—Reeve, 1858: *Littorina* sp. 100 (not Lamarck, 1822; in part; fig. 100 is *Echinolittorina ziczac* (Gmelin, 1791), also includes *Littoraria mauritiana*). Angas, 1867: 209 (not Lamarck, 1822; in part; includes *Littoraria mauritiana*). Smith, 1884: 60–61 (not Lamarck, 1822; in part; includes *Austrolittorina antipodum*). Gatliff, 1887: 60 (not Lamarck, 1822). Tate & May, 1901: 389 (in part; includes *Afrolittorina praetermissa*). Pritchard & Gatliff, 1902: 909–91 (not Lamarck, 1822; in part; includes *Littoraria mauritiana, A. antipodum*).

Littorina (Melarhaphe) mauritiana.—Tryon, 1887: 247, pl. 44, figs. 72, 73, 75 (as *Melaraphe*; not Lamarck, 1822; in part; figs. 70, 74 are *A. cincta*; fig. 71 is *E. ziczac*; also includes *A. antipodum, L. mauritiana*).

Littorina diemenensis var. *mauritiana*.—Etheridge, 1889: 24 (not Lamarck, 1822).

Melarhaphe mauritiana.—Iredale, 1912: 223 (not Lamarck, 1822).

Litorina diemensis Philippi, 1847:195, 196, *Litorina* pl. 4, fig. 1 (unjustified emendation of *Littorina diemenensis* Quoy & Gaimard, 1833, because original spelling is quoted, and emended spelling is used twice and in index; in part; includes *Austrolittorina antipodum*). Küster, 1856: 18, pl. 2, figs. 23–24 (in part; includes *A. antipodum*). Weinkauff, 1878: 31. Weinkauff, 1883: 218 (in part; includes *A. antipodum, A. cincta, Echinolittorina novaezelandiae* [Reeve, 1857]).

Litorina mauritiana var. *crassior* Philippi, 1847: 165; *Litorina* pl. 3, figs. 15, 17a [Cuba (fig. 15); other localities mentioned (not specifically for var. *crassior*) are Mauritius; Nova Hollandia (Australia); Ducee's Island (Ducie Island); restricted to Australia (Rosewater, 1970); lectotype (here designated) Philippi, 1847: fig. 17 (left; 17a in text); in part; fig. 15 is said to come from Cuba and therefore probably *Echinolittorina ziczac* (Gmelin, 1791), probably also includes *Littoraria mauritiana* (Lamarck, 1822)].

Littorina africana.—Reeve, 1857: *Littorina* sp. 37, pl. 8, figs. 37a,b (not Krauss, in Philippi, 1847; in part; includes *Afrolittorina africana*).

Littorina laevis.—Reeve, 1858: *Littorina* sp. 95, pl. 17, fig. 95 (not Philippi, 1846 = *Littoraria mauritiana*).

Littorina caerulescens.—Tenison Woods, 1879: 65–72 (as *coerulescens*; not *Turbo caerulescens* Lamarck, 1822 = *Melarhaphe neritoides* (Linnaeus, 1758); in part; includes *A. antipodum, Afrolittorina praetermissa, A. africana, Littoraria mauritiana, L. undulata* (Gray, 1839), *M. neritoides*).

Littorina diemenensis var. *pseudolaevis* Nevill, 1885: 141 (New South Wales; Port Jackson [Sydney Harbour, New South Wales]; types in ZSI, not seen).

Taxonomic history. This species has a complex taxonomic history, owing to longstanding confusion with several littorinids with similar smooth, white shells. Although the species was first described by Gray in 1826, for the rest of the century the name *Littorina unifasciata* was generally considered a junior synonym of *Littorina mauritiana*. The misidentification of the present species as *L. mauritiana* originated with Philippi (1847), who was deceived by Lamarck's (1822) inadequate description of *Phasianella mauritiana* and by Delessert's (1841) poor figure of one of Lamarck's shells, which does indeed resemble *A. unifasciata*. The species described by Lamarck (1822) is an endemic of Mauritius and the southwestern Indian Ocean, as correctly recognized by Nevill (1885; see Rosewater, 1970, for detailed discussion and lectotype designation), and now classified as a species of *Littoraria* (Reid, 1986). Philippi's (1847) concept of *Litorina mauritiana* may not have included actual specimens of *Littoraria mauritiana* (although he did refer to Delessert's figure), because he had himself described that species as *Littorina laevis* Philippi, 1846, from an unknown locality, and figured it accurately in his monograph (Philippi, 1847: *Litorina* pl. 6, fig. 6). Nevertheless, his concept did not include *A. unifasciata* alone. He recognized two named varieties, *Litorina mauritiana* var. *crassior* and var. *gracilior*. One of the two figures of var. *crassior* (fig. 17a) is a typical shell of *A. unifasciata*, but the other (fig. 15) was said to come from Cuba. The latter figure is indeterminate, but if the locality is correct then it can only be *Echinolittorina ziczac*. Philippi's var. *gracilior* was illustrated by a single figure (fig. 17b); the original shell from the Cuming Collection has been discovered in the BMNH and is undoubtedly a specimen of *E. ziczac*, distinguished by its elongate shape, almost smooth surface and two white bands within the aperture. Shells of *E. ziczac* with the normal zigzag pattern are distinctive, but occasional white shells such as this one do bear a superficial resemblance to *A. unifasciata*. An incomplete accompanying label in Philippi's hand bears the name "*L. mauritiana* from the Isle of Jua—". This is interpreted as "Juan Fernández", and the two other specimens in the syntypic series are probably *A. fernandezensis* (distinction from *A. unifasciata* based on shells alone is sometimes impossible). It appears, then, that Philippi based his *L. mauritiana* var. *gracilior* on a mixture of *E. ziczac* and *A. fernandezensis*, both of which are indeed usually more elongate than typical *A. unifasciata*. It is curious that neither the locality nor Cuming are mentioned by Philippi in his brief remark on var. *gracilior*. However, among the localities for *Litorina mauritiana* he lists "insula Ducee's in Oc. Pacifico (Cuming)". This is a reference to Ducie Island in Polynesia, where none of these species occurs. Conceivably, Philippi may have confused the two Pacific localities of Ducie Island and the Juan Fernández Islands. Following Philippi's (1847) misuse of the name *L. mauritiana*, the name was generally applied to the Australian species and *unifasciata* only returned to common use after the differences between the species of Gray and Lamarck were pointed out by Iredale (1915).

Austrolittorina unifasciata has also sometimes been known by the name *Littorina diemenensis* Quoy & Gaimard, 1833. These authors described their species from Australia, l'île de Van-Diémen (i.e. Tasmania) and New Zealand, and therefore must have included not only *A. unifasciata* but also *A. antipodum*, for only the latter occurs in New Zealand. However, all known type specimens are *A. unifasciata*, in agreement with the type locality that was restricted to Tasmania by Rosewater (1970). Philippi (1847) accepted *L. diemenensis* as a distinct species (and was followed by Küster, 1856; Weinkauff, 1878, 1883), but distinguished it from his concept of *L. mauritiana* only by its smaller size. Philippi also described a still smaller species, found only in New Zealand, as *Litorina antipodum*. Nevertheless, confusion between *A. unifasciata* and *A. antipodum* continued and the two were considered conspecific by several subsequent authors (see Taxonomic History of *A. antipodum*).

The white-shelled, mainly large, Southern Hemisphere littorinids have often been combined as a single species. Tenison Woods (1879) first expressed this view, and in its most extreme form, combining *A. unifasciata, A. antipodum, Afrolittorina praetermissa, Afrolittorina africana, Littoraria mauritiana* and even the European *Melarhaphe neritoides* into a single taxon for which he used the name *Littorina caerulescens* (= *M. neritoides*). This choice of name was justified by quoting Deshayes (1843), although in fact the quote was from Quoy & Gaimard (1833), who compared their *L. diemenensis* with *L. caerulescens* and concluded that they were distinct. Tryon (1887) also had a broad concept, including *A. unifasciata, A. antipodum, A. cincta*

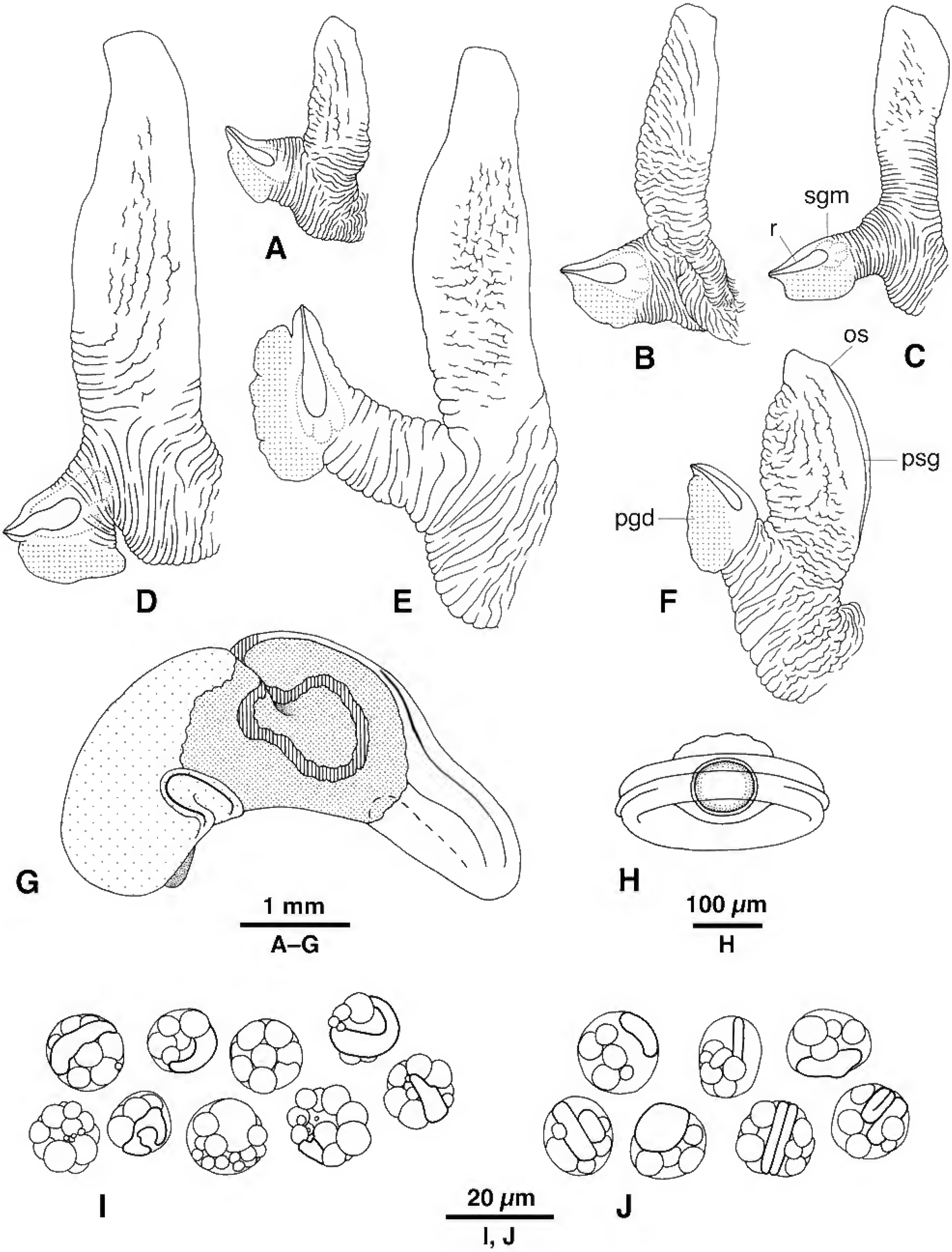

Fig. 7. *Austrolittorina unifasciata*: (*A–F*) Penes. (*G*) Pallial oviduct. (*H*) Egg capsule (after Rudman, 1996). (*I,J*) Paraspermatozoa from two specimens. (*A,B,I*) Blackmans Bay, Tasmania, Australia (BMNH 20030401). (*C*) Nongarrup, Albany, Western Australia (BMNH 20030402). (*D*) Lord Howe Island (AMS C356440). (*E*) Thompson Memorial Park, Lord Howe Island (BMNH 20030403). (*F,J*) North Harbour, Sydney, NSW, Australia (BMNH 20030404). (*G*) Mollymook, NSW, Australia (BMNH 20030393). (*H*) Harbord, Sydney, NSW, Australia. Shell heights: (*A*) 6.6 mm, (*B*) 6.7 mm, (*C*) 9.7 mm, (*D*) 15.7 mm, (*E*) 20.0 mm, (*F*) unknown, (*G*) 10.5 mm. Abbreviations: (*os*) subterminal opening of penial sperm groove; (*pgd*) penial glandular disc (subepithelial glandular material visible by transparency); (*psg*) penial sperm groove; (*r*) receptacle of mamilliform penial gland (visible by transparency); (*sgm*) subepithelial glandular material of mamilliform penial gland (visible by transparency). Shading conventions as in Fig. 3.

and *Littoraria mauritiana* under the name *Littorina mauritiana*. In his monograph of the Indo-Pacific members of the family, Rosewater (1970) recognized three subspecies of *Littorina unifasciata*, the typical one from Australia, subsp. *antipodum* from New Zealand, and subsp. *fernandezensis* from the Juan Fernández Islands. Kilburn (1972) went further, suggesting that *Afrolittorina africana* was probably an additional subspecies of this supposed circumpolar taxon. Only in 1989 were these taxa all listed as distinct species, although without formal redescription (Reid, 1989).

The types of Nevill's var. *pseudolaevis* have not been examined, but he cited Reeve's (1858) fig. 95, which is *L. unifasciata*.

Bandel & Kadolsky (1982) included *Litorina cubana* Weinkauff, 1882 in the synonymy of *L. unifasciata*, citing the spiral sculpture and lack of colour markings, and accordingly corrected its type locality to Australia. However, the original description also mentioned a turreted spire and two pale bands within a brown aperture; these features are never seen in *L. unifasciata*, and unequivocally identify this species as *Echinolittorina ziczac*. This western Atlantic species does occasionally show spiral striae and absence of colour pattern, and it occurs in Cuba. The original figure of Weinkauff (1882: pl. 9, figs. 2–3) is unrecognizable, and types are presumed lost, but the author cited plate 3, figure 17 of Philippi (1847), which is of *L. unifasciata* and *E. ziczac*, as discussed above.

Diagnosis. Shell moderately large; sculpture of spiral striae; white with indistinct broad band of blue-grey above periphery. Penis with broad, wrinkled filament; glandular disc and mamilliform gland on base. Pallial oviduct with two consecutive loops of egg groove, in albumen and capsule glands.

Material examined. 167 lots (108 AMS, 31 USNM, 19 BMNH, 2 IRSNB, 3 ZMA, 2 MNHNP, 2 NMW), including 18 penes, 7 sperm samples, 7 pallial oviducts, 4 radulae.

Shell (Fig. 6, 25A,B). Mature shell height 3 (Nwe, 1974) to 24.9 mm. Shape turbinate to tall-spired (H/B = 1.23–1.83; SH = 1.25–2.16); spire outline straight to slightly convex; whorls gently rounded, suture slightly impressed, periphery slightly angled; solid. Columella pillar slightly concave; columella slightly excavated; eroded parietal area present; outer lip of aperture usually minutely lirate just within margin. Sculpture of 10–12 primary spiral grooves above periphery, that remain as equidistant incised lines throughout growth of shell, continuing faintly on base, occasionally becoming obsolete on final whorl; strong spiral microstriae cover surface; surface, especially spire, often eroded; growth lines weak. Protoconch rarely preserved, 0.36 mm diameter, 3 whorls. Colour white with a more or less distinct broad band of blue-grey above periphery; apex brownish, second and third whorls of teleoconch marked by 5–9 fine spiral brown lines on grey ground (Fig. 25A,B), but lined pattern always disappears on larger shells; aperture dark brown with basal white band.

Animal. Head and sides of foot black; tentacles grey to black, usually with indistinct transverse lines, sometimes a paler longitudinal streak, unpigmented around eye only. Opercular ratio 0.37–0.53. Penis (Fig. 7A–F): filament approximately 0.6–0.7 total length of penis, but not distinctly demarcated from wrinkled base, broad, sometimes swollen, bluntly pointed, surface with reticulate wrinkles (in life and preserved); sperm groove opens subterminally; single large, often narrow, mamilliform gland and adjacent flap of penial glandular disc borne together on lateral branch of base; penis unpigmented; penis does not show annual regression (Nwe, 1974; Underwood, 1974). Euspermatozoa 61–69 µm; paraspermatozoa (Fig. 7I,J) are spherical clusters of large spherical granules, 13–17 µm diameter, usually with 1–2 rod bodies of short cylindrical or arcuate or irregular shape (occasionally indistinct or possibly absent), not projecting from cell. Pallial oviduct (Fig. 7G) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, opaque pink, within which portion adjacent to egg groove (translucent capsule gland) is differentiated as a ring; copulatory bursa confined to straight section of pallial oviduct, opening near anterior end.

Spawn and development. Spawn (Fig. 7H) a transparent pelagic capsule 240 µm diameter containing a single ovum 100 µm diameter, capsule with roughened dome surrounded by circumferential skirt with median ridge described from Sydney by Rudman (1996); smaller capsules 100–140 µm, with ovum 80 µm, described from vicinity of Adelaide by Nwe (1974); development planktotrophic; breeding throughout the year near Adelaide (Nwe, 1974); year-round recruitment recorded in Tasmania (Chen & Richardson, 1987); females mature from October to May at Cape Banks (NSW) with peak spawning from December to March (Underwood, 1974).

Radula (Fig. 4C,D). Relative radular length 3.5–4.8. Rachidian: length/width 1.21–1.62; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded at tip or rectangular. Outer marginal: 6–8 cusps.

Habitat. This species is ubiquitous and abundant on most of the temperate shores of Australia and has been included in numerous ecological surveys and field experiments. It can be found on any hard substrate, including schist, granite, sedimentary rock, concrete and even wooden piers (Nwe, 1974). On exposed coasts it is abundant in the littoral fringe up to the highest level of spring tides (reaching higher levels with stronger wave action) and in the upper barnacle zone, whereas juveniles are present at lower levels among barnacles and *Pyura* (Dakin *et al.*, 1948; Guiler, 1951; Bennett & Pope, 1953, 1960; Underwood, 1981; Wells, 1984; Chen & Richardson, 1987). On sheltered shores it extends lower, almost to low water of neap tides (Endean *et al.*, 1956), but is absent from sites of extreme shelter (Guiler, 1952a; Womersley & Edmonds, 1958; Branch & Branch, 1981). Densities can be remarkably high on shores of moderate exposure (to 9600 m^{-2} at Cape Banks, NSW), resulting in extreme intraspecific competition for food (Branch & Branch, 1981). On a small scale, the species shows a patchy distribution both within and between shores, but some trends have been identified: snails are largest in the upper and lowermost parts of the tidal range, and density is negatively correlated with size; animals are clustered in pits and crevices, and are more common on horizontal surfaces and where barnacles are present; there is no relation between density and exposure of the shore (Britton *et al.*, 1991; Chapman, 1994a; Underwood & Chapman, 1996). The food consists of microalgae, sporelings and lichens (Branch & Branch, 1981; Jernakoff, 1983). Detailed studies of

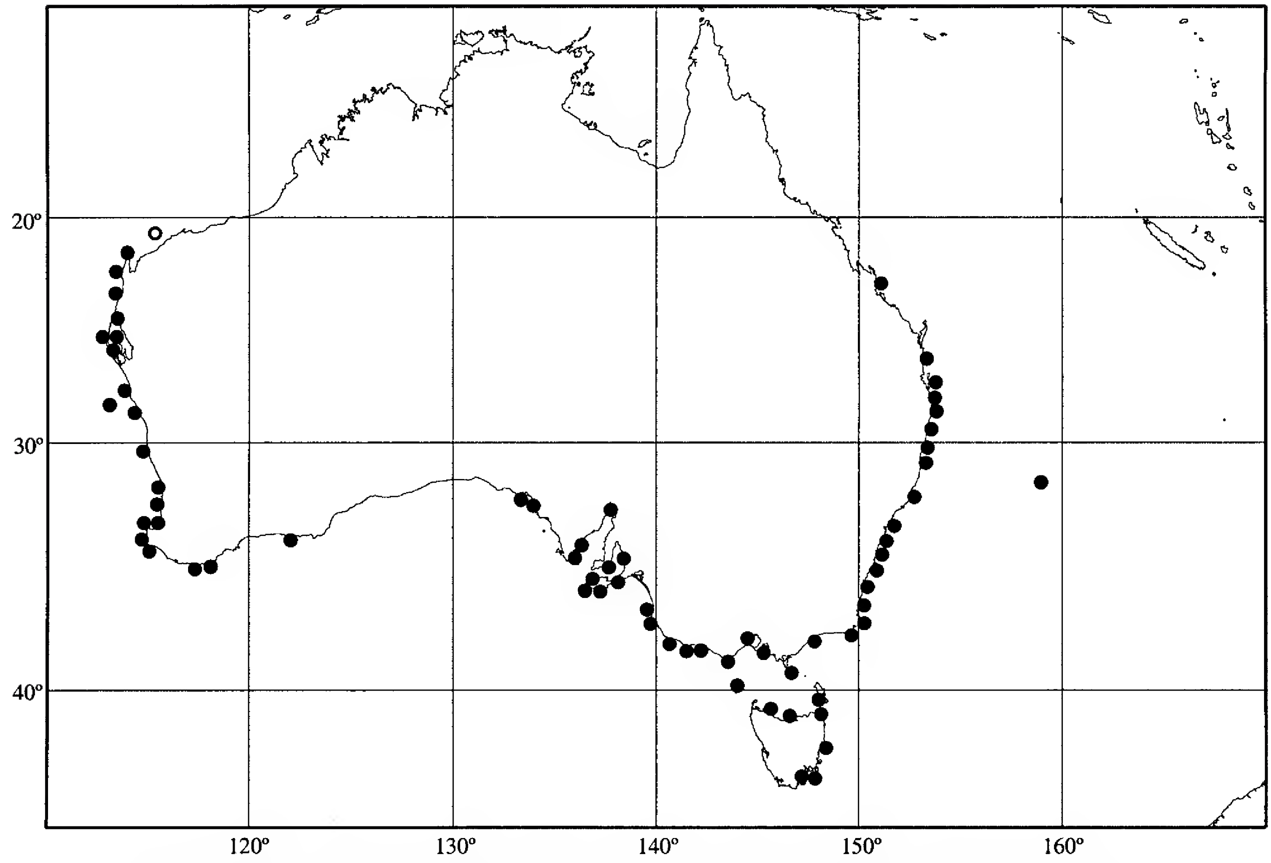

Fig. 8. Distribution of *Austrolittorina unifasciata*. Open circle is a record from F.E. Wells (pers. comm.).

movement (Underwood & Chapman, 1985, 1989), foraging (Chapman, 2000), behaviour following transplant (Chapman, 1986, 1999), dispersion in relation to microtopography (Underwood & Chapman, 1989, 1992) and aggregation behaviour (Chapman, 1995b, 1998; Chapman & Underwood, 1996) have been done in New South Wales. Over its extensive geographical range, it is microsympatric with *N. pyramidalis* in New South Wales and southern Queensland (but that species extends higher in the littoral fringe), with *Afrolittorina praetermissa* in Victoria, Tasmania and South Australia (but that species occurs at lower levels, in more cryptic habitats, and is common on more sheltered shores), and with *Echinolittorina australis* (Gray, 1826) in Western Australia.

Range (Fig. 8). Temperate and subtropical coastline of Australia, Tasmania and Lord Howe Island. In Western Australia there are numerous records as far north as North West Cape (21°45'S 114°10'E, AMS C387269), which was given as the northwestern limit of this species by Wells (1980), and a single specimen from Barrow Island is present in WAM (F.E. Wells, pers. comm.). There is a record from still further north at Cape Keraudren (19°57'S 119°45'E, coll. F. Haddrill, 1976, AMS C389557), but this is considered doubtful (F.E. Wells, pers. comm.). A lot from Vansittart Bay in the far north of WA (Coll. W. Burrows, AMS C45183) is certainly unreliable (this may perhaps be the source of the northwestern extralimital record on the distribution map by Rosewater, 1970: pl. 362). There are no records from the Great Australian Bight between the Archipelago of the Recherche, WA (34°15'S 112°50'E, AMS C69337) and Point Sinclair, SA (32°06'S 133°00'E, AMS C387947), but this is probably a collecting artefact resulting from the inaccessibility of this coastline. Further east there are abundant records from the coastlines of South Australia, Victoria, Tasmania and New South Wales, as far north as Point Cartwright and Noosa Heads in southern Queensland (26°23'S 153°09'E, AMS C386963, C107999). Endean *et al.* (1956) noted that the northern limit in Queensland was associated with wave action; at Noosa and southwards the species was abundant on exposed shores, but to the north it was replaced on sheltered shores by *Echinolittorina vidua* (Gould, 1859) (as *Melarhaphe melanacme*). Only a single reliable lot has been seen from further north, at Yeppoon (23°08'S 158°44'E, 6 specimens, collected in 1952, AMS C387974), and this is also an exposed locality; to the north the coast is sheltered by the Great Barrier Reef. Rosewater (1970: pl. 362) plotted a record in the vicinity of Cooktown, but gave no details in the text and this record is considered unreliable. The species is common on Lord Howe Island (5 lots AMS, 3 lots BMNH), where shells reach unusually large size, and there is a single record from Elizabeth Reef (29°56'S 159°04'E, USNM 767443, not seen). In Tasmania it is common on the east coast and islands of Bass Strait, sporadic on the sheltered north coast and in the south, but is absent from the exposed west coast (Bennett & Pope, 1960; contrary to Kershaw, 1958, who may have confused the species with *Afrolittorina praetermissa*). Whether this absence from western Tasmania is a consequence of the strong exposure, or of the low sea temperatures produced by the cold current of the West Wind Drift, is not known.

Remarks. The size and shape of the shell show significant variation (Fig. 6). Size gradients on the shore have been mentioned above; adult size has been said to be larger in either sheltered (Nwe, 1974) or exposed sites (Branch & Branch, 1981), but no consistent correlation of size with wave-exposure was found in a well-replicated survey of shores at Cape Banks, New South Wales (Chapman, 1994a). As in many littorinids, sexual dimorphism has been reported, the males being smaller (Nwe, 1974). An early study at a single site reported a relatively larger shell aperture on the exposed side of a wall (Bassingthwaighte & Foulds, 1985), but although supported by at least one comparison between shores of contrasting exposure (Chapman, 1997), this may not be a general pattern (McMahon, 1992). Indeed, Chapman (1995a) emphasized that variation in shape within shores was as great as that between shores, and found no consistent correlations with density, size or exposure; the only consistent pattern was a decrease in relative aperture size at higher levels on the shore. Functional interpretations of intraspecific variation in littoral gastropods have suggested that tall shells with small apertures contain and conserve larger reserves of water, that these are more resistant to crushing by predators, and that enlarged apertures improve tenacity when wave action is strong. However, experimental tests failed to support these suggestions for *A. unifasciata* (Chapman, 1997). The planktotrophic mode of larval development implies high gene flow within and between nearby shores, so it is likely that the differences described are the result of phenotypic plasticity rather than genotypic adaptation (McMahon, 1992; Chapman, 1995a). One possibility is a direct effect of growth rate (determined by time available for feeding) on shell shape; slower growth at high levels on the shore might produce the more elongate form (Chapman, 1997).

This well-known species is unlikely to be confused with any of the littorinids with which it is sympatric. Shells of *A. fernandezensis*, endemic to the Juan Fernández and Desventuradas Islands off Chile, are so similar that they are sometimes indistinguishable; usually they are slightly more elongate than *A. unifasciata* and the margin of the aperture is more distinctly lirate. Shells of *A. antipodum*, found in New Zealand, are smaller, more tall-spired and have a more pronounced bluish peripheral band (see Remarks on *A. antipodum*). The penes of all three species are diagnostic.

The molecular analysis of Williams *et al.* (2003) showed that the sister species of *A. unifasciata* is *A. fernandezensis*. The authors explained this interesting trans-Pacific relationship as a case of dispersal from Australia to the east, because the estimated age of the divergence (13–30 million years) was later than the breakup of Gondwana that might have provided a vicariant explanation. They did, however, point out that the distance across the Pacific is too great for larval dispersal under the present-day current regime, so that it may have been accomplished by use of formerly emergent seamounts as stepping stones.

Austrolittorina fernandezensis (Rosewater, 1970)

?*Litorina mauritiana* var. *gracilior* Philippi, 1847: 165 (no locality in text; 3 syntypes BMNH 20020038 plus 20020039; in part; 2 syntypes probably this species, but largest syntype, figured by Philippi, 1847: *Litorina* pl. 3, fig. 17b, is *Echinolittorina ziczac*).

Littorina (Austrolittorina) unifasciata fernandezensis Rosewater, 1970: 471–472, pl. 359, figs. 9–12, pl. 361, fig. B (radula), pl. 363 (distribution) (east shore of Cumberland Bay, Isla Más a Tierra, Juan Fernández Islands [Chile]; holotype USNM 368900, Rosewater, 1970, pl. 359, figs. 11–12, seen; 25 paratypes USNM 679256, seen; 11 paratypes DMNH 039221, not seen).

Nodilittorina (Austrolittorina) fernandezensis Reid, 2002*a*: 151–154, figs. 18Q–V, 20 (distribution), 21G–J (penes), L (pallial oviduct), O, P (paraspermatozoa), 22C, D (radula).

Austrolittorina fernandezensis.—Williams *et al.*, 2003.

Taxonomic history. For full synonymy, see Reid (2002*a*). As discussed above (see Taxonomic History of *A. unifasciata*) the name *Litorina mauritiana* var. *gracilior* Philippi, 1847 was probably partly based on this species, although this is speculative. To exclude this name from the synonymy of *A. fernandezensis*, the largest figured syntype (BMNH 20020038), which is undoubtedly a specimen of *E. ziczac*, is here designated lectotype.

Diagnosis. Shell large; spiral sculpture of fine microstriae; aperture finely lirate; white with broad indistinct blue-grey zone above periphery. Penial filament small, pointed; small mamilliform gland and large glandular disc on base. Pallial oviduct with two consecutive loops of egg groove, in albumen and capsule glands.

Range. Juan Fernández Islands and Desventuradas Islands, southeastern Pacific Ocean.

Remarks. See Remarks on *A. unifasciata* for distinction from that species.

Austrolittorina antipodum (Philippi, 1847)

Figs. 4E,F, 9–11

Littorina diemenensis Quoy & Gaimard, 1833: 479–480 (in part; not *L. diemenensis* Quoy & Gaimard, 1833 = *A. unifasciata*). Reeve, 1858: *Littorina* sp. pl.17, fig. 94 (not Quoy & Gaimard, 1833). Hutton, 1878: 27 (not Quoy & Gaimard, 1833).

Litorina diemensis.—Philippi, 1847:195, *Litorina* pl. 4, fig. 1 (not *L. diemensis* Philippi, 1847, emendation of *Littorina diemenensis* Quoy & Gaimard, 1833 = *A. unifasciata*; in part; includes *A. unifasciata*). Weinkauff, 1883: 218 (in part; includes *A. unifasciata, A. cincta, Echinolittorina novaezelandiae*).

Litorina antipodum Philippi, 1847: 195–196, *Litorina* pl. 4, fig. 2 (New Zealand; lectotype, here designated, Philippi, 1847: *Litorina* pl. 4, fig. 2; fig. 9D herein). Weinkauff, 1882: 61–62, pl. 8, fig. 4.

Littorina (Melarhaphe) antipodum.—Adams & Adams, 1854: 314 (as *Melaraphe*).

Littorina antipodum.—Nevill, 1885: 143.

Littorina (Austrolittorina) unifasciata antipodum.—Rosewater, 1970: 423 (as *antipoda*), 470–471, pl. 359, figs. 6–8, pl. 360, fig. 5, pl. 362 (distribution). Powell, 1976: 87, pl. 16, fig. 12. Powell, 1979: 87, pl. 23, fig. 9.

Nodilittorina (Nodilittorina) antipodum.—Reid, 1989: 99.

Nodilittorina antipodum.—Spencer & Willan, 1996: 18.

Nodilittorina (Austrolittorina) antipodum.—Reid, 2002*a*: 154.

Austrolittorina antipodum.—Williams *et al.*, 2003.

Littorina caerulescens.—Tenison Woods, 1879: 65–72 (as *coerulescens*; not *Turbo caerulescens* Lamarck, 1822 = *Melarhaphe neritoides*; in part; includes *A. unifasciata, Afrolittorina praetermissa, A. africana, Littoraria mauritiana, M. neritoides*). Hutton, 1880: 79 (not Lamarck, 1822; in part; includes *A. unifasciata*). Hutton, 1882: 164, pl. 7, fig. E (radula; not Lamarck, 1822).

Littorina mauritiana.—Smith, 1884: 60–61 (not *Phasianella mauritiana* Lamarck, 1822 = *Littoraria mauritiana*; in part; includes *A. unifasciata*). Suter, 1901: 214 (not Lamarck, 1822).

Iredale, 1910: 70–71 (not Lamarck, 1822).

Littorina (Melarhaphe) mauritiana.—Tryon, 1887: 247 (as *Melaraphe*; not Lamarck, 1822; includes *A. unifasciata, A. cincta, L. mauritiana, Echinolittorina ziczac*).

Litorina (Melarhaphe) mauritiana.—Suter, 1913: 188, pl. 38, fig. 28 (not Lamarck, 1822; includes *A. unifasciata, L. mauritiana*; as *Melaraphe*; as *Littorina mauritiana* in Atlas, 1915).

Litorina mauritiana.—Bucknill, 1924: 37, pl. 7, fig. 22.

Melarhaphe unifasciata.—Iredale, 1915: 447 (not *Littorina unifasciata* Gray, 1826 = *A. unifasciata*; in part; includes *A. unifasciata*). Oliver, 1915: 518 (not Gray, 1826).

Melarhaphe zelandiae.—Finlay, 1928: 241 (not Finlay, 1927 = *A. cincta*).

Melarhaphe oliveri Finlay, 1930: 224–225 (Hampden, east coast of South Island, New Zealand; holotype Auckland Museum AK 70456 (formerly TM456) plus 1 paratype AK 72574 (formerly TM456), not seen). Powell, 1937: 67, pl. 9, fig. 12. Powell, 1962: 83, pl. 9, fig. 12 (as *Melarhapha*). Morton, 1975: fig. 6a–c (radula), fig. 7a,b (stomach).

Melarapha oliveri.—Dell, 1963: 225.

Taxonomic history. There has been a long history of inclusion of this species as a single taxon with the Australian *A. unifasciata*, and sometimes also with other superficially similar white-shelled littorinids (see Taxonomic History of *A. unifasciata*). Quoy & Gaimard (1833) listed the locality New Zealand for their species *L. diemenensis* and therefore evidently considered the Australian and New Zealand species to be the same (although the name has now been restricted to *A. unifasciata*). This concept was followed by Philippi (1847), although in addition he introduced *Litorina antipodum* for smaller, taller-spired, less markedly striated shells with a dark peripheral band, found in New Zealand. This name was almost entirely neglected for 120 years (exceptions were Weinkauff, 1882; Nevill, 1885), until used as a subspecies of *L. unifasciata* by Rosewater (1970). Instead, the species was generally combined with *A. unifasciata* under the name *L. mauritiana* (Smith, 1884; Suter, 1901, 1913; Iredale, 1910; Bucknill, 1924). Following Iredale (1915), the name *Melarhaphe unifasciata* was briefly used in New Zealand (Oliver, 1915). Iredale (1915) had also suggested that "the Neozelanic shell may prove subspecifically separable", which induced Finlay (1927) to introduce the new name *M. zelandiae*. However, as Finlay (1930) later confessed: "Owing ... to a curious and unpardonable misconception of species I described the wrong shell" (the description applied to the other New Zealand littorinid, *A. cincta*). He therefore introduced yet another name, *M. oliveri*, for the present species, which was widely used in New Zealand (e.g., Powell, 1937, 1962; Dell, 1963). This was superseded by the older name *L. unifasciata antipodum* following the revision by Rosewater (1970). The taxon was given full specific status in the worldwide family list of Reid (1989), although the anatomical evidence justifying this decision was not presented. Rudman (1996) noted that the differences between the egg capsules of *A. unifasciata* and *A. antipodum* supported separate species status for both.

No type specimens of *Litorina antipodum* are known to exist, and to obviate any further confusion as to the identity of the taxon Philippi's (1847) figure is here designated lectotype. The shape and coloration of the shell leave no doubt as to its identity (Fig. 9D). The specific epithet is a noun in the genitive case, not an adjective that should agree in gender with the feminine generic name (e.g., Rudman, 1996).

It may be noted that *Littorina novaezelandiae* Reeve, 1857 was mistakenly said to come from New Zealand in its original description; it is a valid species of *Echinolittorina* that is endemic to Sri Lanka (Reid, 2001).

Diagnosis. Shell small, usually tall-spired, often smooth; white with broad band of blue-grey above periphery. Penis with smooth, slightly swollen filament; glandular disc and mamilliform gland on base. Pallial oviduct with two consecutive loops of egg groove, in albumen and capsule glands.

Material examined. 76 lots (15 AMS, 18 USNM, 14 BMNH, 4 IRSNB, 4 ZMA, 1 MNHNP, 1 NMW, 19 MNZ), including 11 penes, 5 sperm samples, 7 pallial oviducts, 3 radulae.

Shell (Fig. 9). Mature shell height 5.4–13.7 mm. Shape high-turbinate to tall-spired (H/B = 1.36–2.20; SH = 1.43–2.63, exceptionally 3.22); spire outline straight to slightly convex; whorls gently rounded, suture slightly impressed, periphery slightly angled; solid. Columella pillar short, slightly concave; columella slightly excavated; small eroded parietal area sometimes present. Sculpture of 9–12 approximately equidistant primary spiral grooves (incised lines) may be present above periphery, continuing faintly on base, but frequently surface is almost smooth; microstriae absent; surface, especially spire, often eroded; growth lines weak. Protoconch rarely preserved, about 3 whorls, 375–425 µm length, sculptured by spiral rows of minute tubercles (Pilkington, 1971). Colour white, with broad spiral blue-grey band above periphery; rarely grey-black with white base, or almost entirely white with faint grey band; small juveniles entirely black or brown, with spiral white line on base; aperture dark brown with basal white band.

Animal. Head, tentacles and sides of foot black. Opercular ratio 0.47–0.61. Penis (Fig. 10A–E): filament 0.5 total length of penis, smooth, bluntly pointed, slightly swollen, sperm groove opens slightly subterminally; single large, often narrow, mamilliform gland and adjacent large flap of penial glandular disc borne together on short lateral branch of base; penial base often with black pigment. Euspermatozoa 75–82 µm; paraspermatozoa (Fig. 10H,I) spherical, 11–14 µm diameter, containing large spherical granules and a curved, twisted or torus-shaped rod body. Pallial oviduct (Fig. 10F) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, within which portion adjacent to egg groove (translucent capsule gland) is differentiated as a ring; copulatory bursa confined to straight section of pallial oviduct, opening near anterior end.

Spawn and development. Spawn (Fig. 10G) a transparent pelagic capsule 200–250 µm diameter, containing a single ovum 80 µm diameter, capsule with hemispherical dome sculptured by 3 concentric rings, peripheral ridge and a basal circumferential flange; development planktotrophic, inferred planktonic life of 1–2 months; spawning season November to March (at Otago; Pilkington, 1971).

Radula (Fig. 4E,F). Relative radular length 2.0–2.5. Rachidian: length/width 1.13–1.33; major cusp elongate, rounded or slightly pointed at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded at tip. Outer marginal: 6–7 cusps.

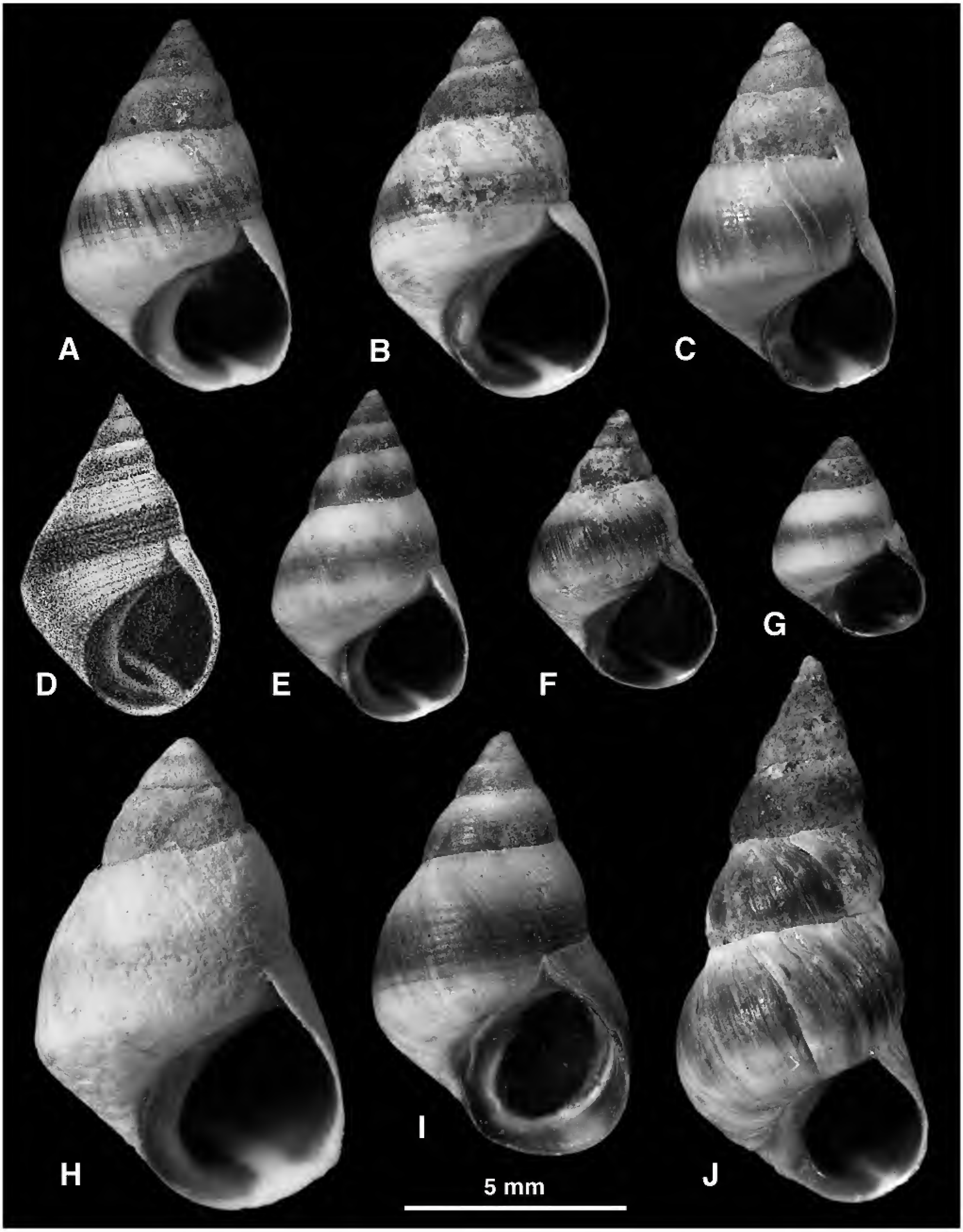

Fig. 9. *Austrolittorina antipodum*: (*A*) Auckland Harbour, New Zealand (BMNH 20030405). (*B,F*) Muriwai, New Zealand (BMNH 20030406). (*C,E*) Island Bay, Cook Strait, New Zealand (USNM 671202). (*D*) lectotype figure of *Litorina antipodum* Philippi, 1847 (Philippi, 1847: *Litorina* pl. 4, fig. 2). (*G*) Long Beach, Russell, New Zealand (BMNH 20030407). (*H*) Great Island, Three Kings Islands, New Zealand (MNZ M049237). (*I*) Raoul Island, Kermadec Islands (MNZ M214380). (*J*) Waitangi, Chatham Islands, New Zealand (MNZ M110492).

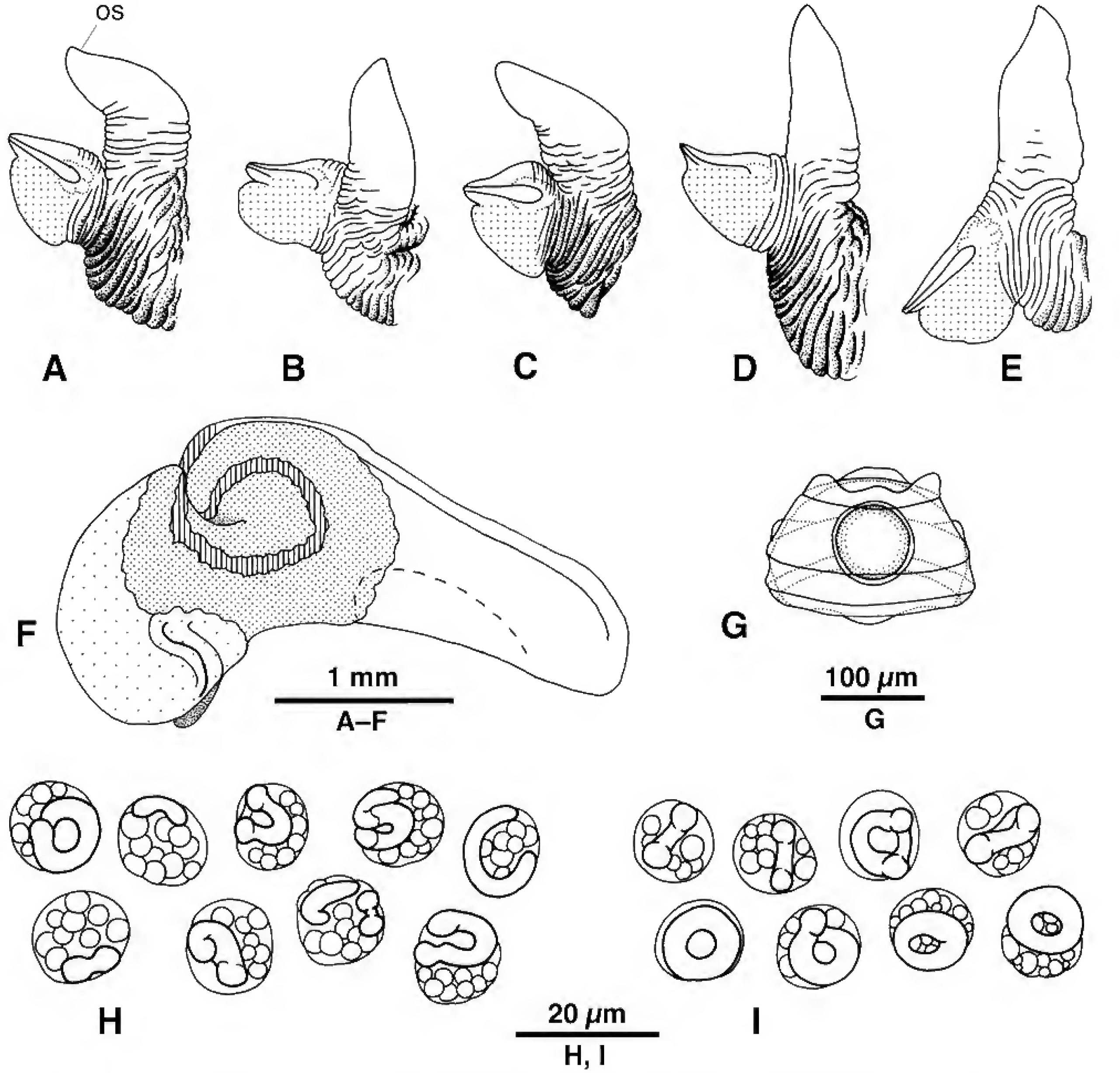

Fig. 10. *Austrolittorina antipodum*: (*A–E*) Penes. (*F*) Pallial oviduct. (*G*) Egg capsule (after Pilkington, 1971). (*H,I*) Paraspermatozoa from two specimens. (*A–C,F,H*) Wellington Harbour, New Zealand (BMNH 20030394). (*D,E,I*) Kaikoura, New Zealand (BMNH 20030408). (*G*) Portobello, Otago Harbour, New Zealand. Shell heights: (*A*) 7.5 mm, (*B*) 7.4 mm, (*C*) 7.4 mm, (*D*) 7.4 mm, (*E*) 8.9 mm, (*F*) 9.8 mm. Abbreviation: (*os*) subterminal opening of penial sperm groove. Shading conventions as in Fig. 3.

Habitat. Throughout much of New Zealand, especially in the north, this species is abundant on rocky shores from the top of the littoral fringe to the upper part of the barnacle zone (EHWST to MTL). Juveniles occur below adults, often among barnacles. The upper limit depends upon shade and spray, so that on the most strongly exposed, shaded vertical cliffs, it can reach 12 m above EHWST. It is less common on sheltered shores, scarce in extreme shelter, and absent where water is turbid. Shaded rock faces are favoured; on sunny faces, it occupies cracks and crevices and it may occur in shallow, high-level rock pools (Dellow, 1950; Knox, 1953; Foster, 1966; Morton & Miller, 1968). In the south of South Island *A. antipodum* is less common and occupies a more restricted vertical range, confined to the littoral fringe, and its distribution is shifted towards more sheltered shores (Batham, 1956, 1958; Morton & Miller, 1968; Pilkington, 1971). At Rangitoto Island (near Auckland), it has been recorded among *Salicornia* and lava blocks on stiff mud (Powell, 1933a). The diet included black lichens, diatoms, *Ulva* and *Enteromorpha* (Powell, 1933a; Morton, 1975). It is frequently sympatric with *A. cincta* (see Habitat of *A. cincta* for comparison).

Range (Fig. 11). New Zealand, Chatham Islands, Kermadec Islands. This species occurs around the entire coastline of North and South Islands, and is also recorded from Stewart Island (Ringaringa, 46°44'S 168°09'E, MNZ M019600), Snares Islands (North Island, 48°02'S 166°36'E, MNZ M015474), Chatham Islands (Waitangi Bay, 43°57'S 176°33'W, MNZ M110471; Powell, 1933), Three Kings

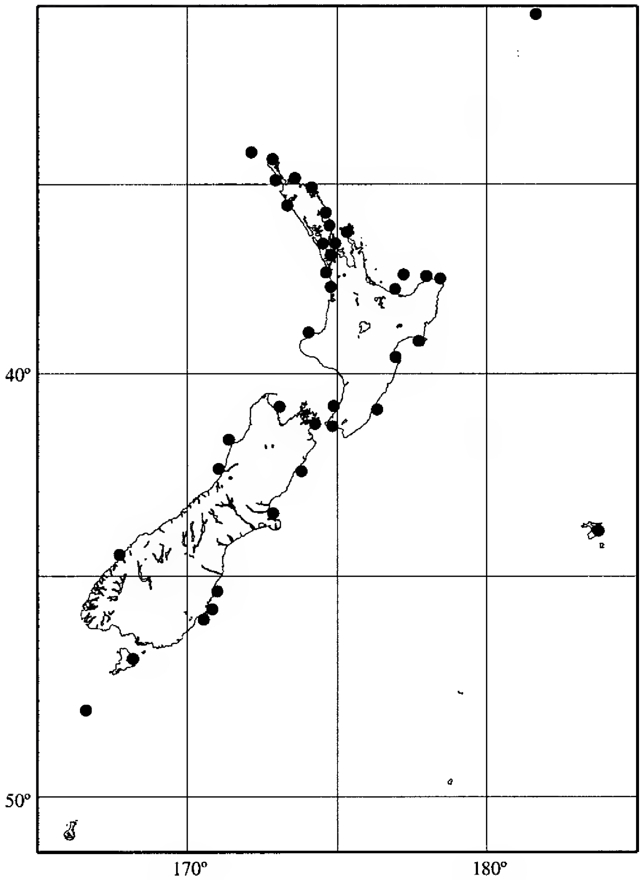

Fig. 11. Distribution of *Austrolittorina antipodum*.

Islands (Great Island, 34°09'S 172°09'E, MNZ 049237) and Kermadec Islands (Raoul Island, 29°16'S 177°55'W, MNZ M 214380, AMS). The species is reported to be rare in the Kermadec Islands (Iredale, 1910; Oliver, 1915; Brook, 1998); it is likely that only chance migrants reach these islands and that the population is not self-sustaining.

Remarks. Although superficially similar to the Australian *A. unifasciata*, these two species should not be confused. *Austrolittorina antipodum* is smaller, reaching only 13.7 mm in height (*A. unifasciata* attains 24.9 mm), more tall-spired, the spiral striae are less marked and often obsolete, microstriae are absent, the peripheral blue-grey band is more conspicuous, and the penial filament is shorter and not wrinkled. In addition, their ranges are allopatric. Throughout most of its range *A. antipodum* is sympatric with *A. cincta*, although it has a more northern distribution. The latter is readily separated by the brown spiral lines of its shell and larger size (to 20.2 mm); anatomically the two are similar, the penial filament of *A. cincta* being only slightly more pointed.

Occasionally shells of *A. antipodum* are found that are extremely elongate (H/B up to 2.21, SH up to 3.22; Fig. 9J); by analogy with other species (see Remarks on *Afrolittorina knysnaensis*) these probably represent specimens infected with trematode parasites, although this has not been confirmed by dissection.

Molecular data have shown that *A. antipodum* and *A. cincta* are sister species, with an estimated divergence time of more than 10 million years. Possible causes of this speciation are unknown; it is too recent to be ascribed to the Oligocene transgression that greatly reduced the land area of New Zealand (Cooper & Millener, 1992). In turn, this pair is sister to the pair *A. unifasciata* plus *A. fernandezensis*, with a separation estimated as 23–44 million years (Williams *et al*., 2003). This is younger than the attainment of the present width of the Tasman Sea, implying that dispersal took place from Australia to New Zealand.

Austrolittorina cincta (Quoy & Gaimard, 1833)

Figs. 4G,H, 12–14

Littorina cincta Quoy & Gaimard, 1833: 481–482, pl. 33, figs. 20–21 (New Zealand; lectotype (Rosewater, 1970) (fig. 12B) plus 2 paralectotypes, MNHNP, seen). Deshayes, 1843: 209–210. Reeve, 1857: *Littorina* sp. 53, pl. 11, fig. 53. Hutton, 1878: 27. Hutton, 1880: 78. Hutton, 1882: 164, pl. 7, fig. D (radula). Nevill, 1885: 143. Suter, 1901: 214–215.

Litorina cincta.—Philippi, 1847: 202, pl. 4, fig. 18. Weinkauff, 1882: 76, pl. 10, figs. 5, 8. Weinkauff, 1883: 222. Watson, 1886: 574. Bucknill, 1924: 37, pl. 7, fig. 23.

Littorina (Melarhaphe) cincta.—Adams & Adams, 1854: 314 (as *Melaraphe*).

Litorina (Melarhaphe) cincta.—Suter, 1913: 187, pl. 38, fig. 27 (as *Melaraphe*; as *Littorina cincta* in Atlas, 1915).

Melarhaphe cincta.—Finlay, 1928: 241 (as *Malarhaphe*). Powell, 1937: 67, pl. 9, fig. 13. Powell, 1955: 74. Powell, 1962: 83, pl. 9, fig. 13 (as *Melarhapha*). Dell, 1963: 225 (as *Melarapha*).

Littorina (Austrolittorina) cincta.—Rosewater, 1970: 423, 473–474, pl. 364, figs. 1–6, pl. 365, fig. A (penis), pl. 366 (distribution). Powell, 1976: 87, pl. 16, fig. 13. Powell, 1979: 87, pl. 23, fig. 10.

Nodilittorina cincta.—Bandel & Kadolsky, 1982: 3. Spencer & Willan, 1996: 18.

Nodilittorina (Nodilittorina) cincta.—Reid, 1989: 99.

Nodilittorina (Austrolittorina) cincta.—Reid, 2002*a*: 154.

Austrolittorina cincta.—Williams *et al*., 2003.

Littorina luctuosa Reeve, 1857: *Littorina* sp. 65, pl. 13, fig. 65 (New Zealand; 3 syntypes BMNH 1968315; Rosewater (1970: pl. 364, figs. 3, 4) figured one as "holotype", but this is not a valid lectotype designation, ICZN, 1999: Arts 74.5, 74.6). Hutton, 1880: 79.

Litorina luctuosa.—Weinkauff, 1882: 72, pl. 9, fig. 12.

Littorina (Melarhaphe) mauritiana.—Tryon, 1887: 247, pl. 44, figs. 70, 74 (as *Melaraphe*; not *Phasianella mauritiana* Lamarck, 1822 = *Littoraria mauritiana*; includes *A. unifasciata, A. antipodum, L. mauritiana, Echinolittorina ziczac*).

Melarhaphe zelandiae Finlay, 1927: 375; pl. 18, figs. 18–19 (Dunedin Harbour, New Zealand; holotype Auckland Museum AK 70457 (formerly TM457) plus 3 paratypes AK 72526 (formerly TM457), not seen).

Taxonomic history. This species is readily recognized by its brown shell and has therefore been correctly identified by most authors. It was redescribed as *Littorina luctuosa* by Reeve (1857), a species incorrectly synonymized with *A. antipodum* (Weinkauff, 1883; Nevill, 1885) until its identity was indicated by Suter (1901, 1913). The species was inadvertently named again by Finlay (1927) as *M. zelandiae* (see Finlay, 1930; see Taxonomic History of *A. antipodum*). This species was included in a very broad concept of *L. mauritiana* by Tryon (1887; see Taxonomic History of *A. unifasciata*).

Diagnosis. Shell moderately large, usually tall-spired, sculptured with incised spiral lines; cream with brown spiral lines, or brown with pale grooves. Penis with bluntly pointed, slightly swollen filament; glandular disc and mamilliform gland on base. Pallial oviduct with two consecutive loops of egg

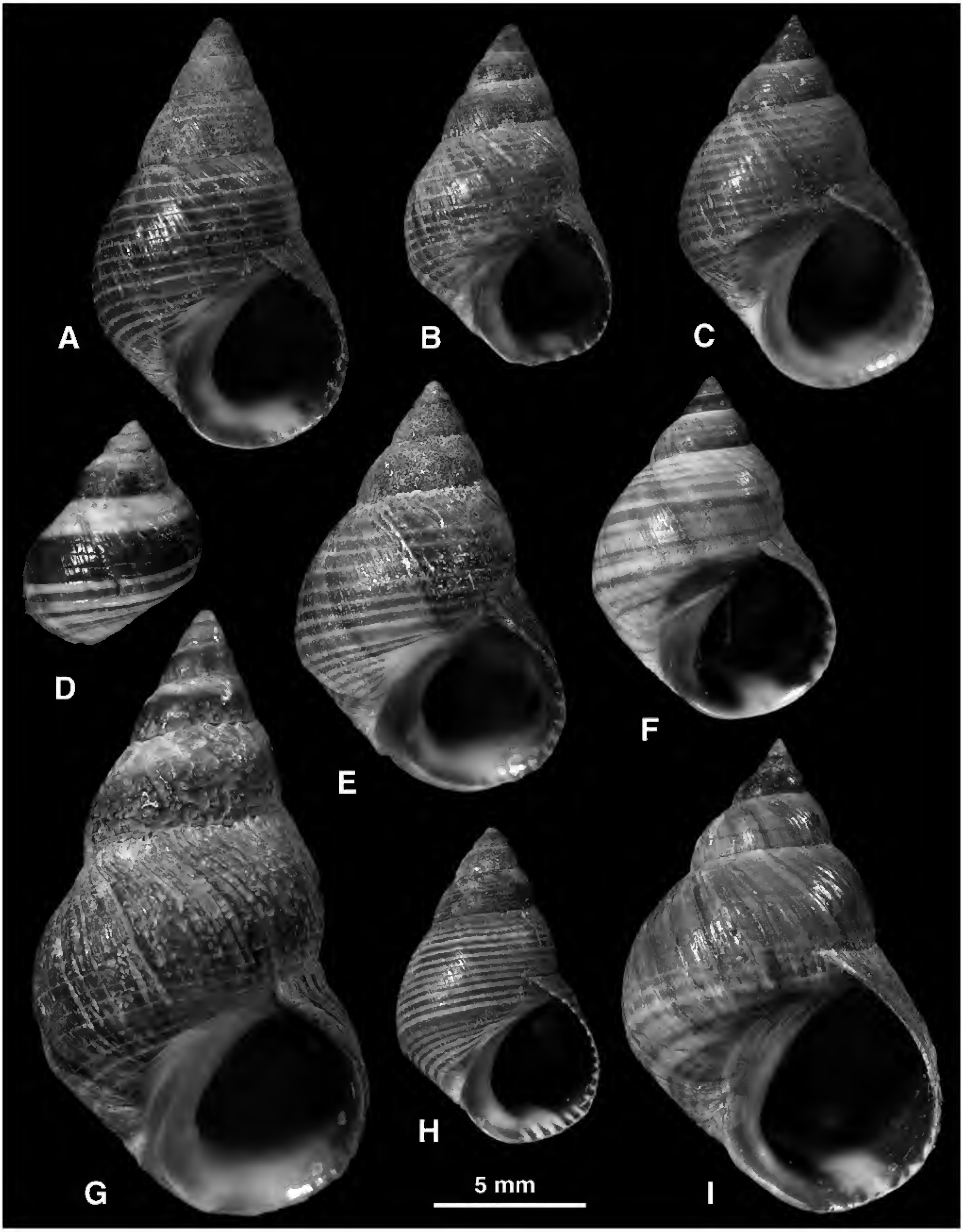

Fig. 12. *Austrolittorina cincta*: (*A,E,H*) Cyathea Cove, Tasman Bay, New Zealand (BMNH 20030409). (*B*) Lectotype of *Littorina cincta* Quoy & Gaimard, 1833 (MNHNP unreg.). (*C*) Muriwai, New Zealand (BMNH 20030410). (*D*) Ringaringa, Stewart Island, New Zealand (MNZ M042428). (*F*) Flat Point, Wairarapa, New Zealand (MNZ M095414). (*G*) Port Waikato, New Zealand (BMNH 20030411). (*I*) New Zealand (BMNH 20030412).

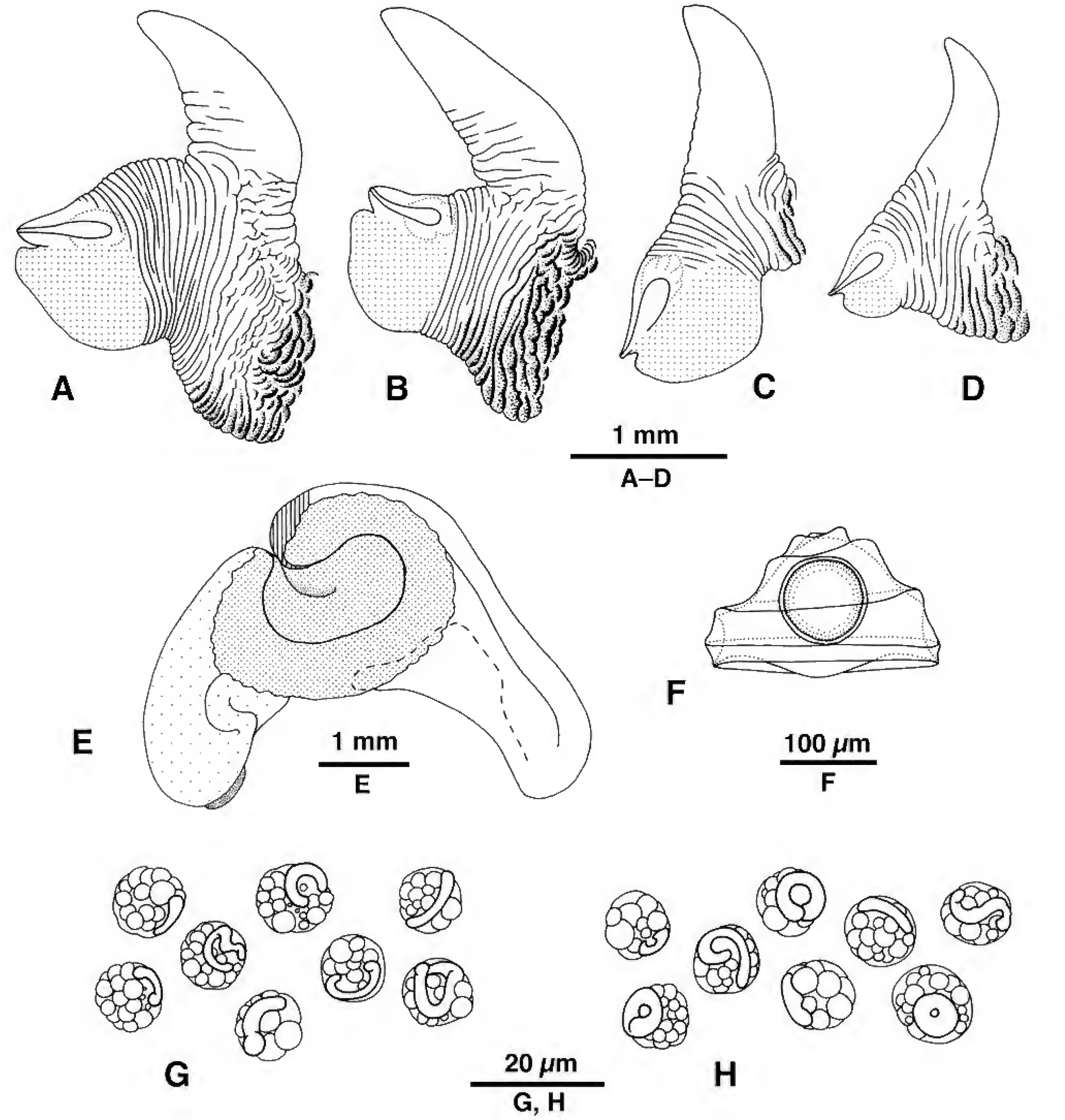

Fig. 13. *Austrolittorina cincta*: (*A–D*) Penes. (*E*) Pallial oviduct. (*F*) Egg capsule (after Pilkington, 1971). (*G,H*) Paraspermatozoa from two specimens. (*A,E,G*) Wellington Harbour, New Zealand (BMNH 20030413). (*B,H*) Kaikoura, New Zealand (BMNH 20030414). (*F*) Portobello, Otago Harbour, New Zealand. Shell heights: (*A*) 12.3 mm, (*B*) 10.4 mm, (*C*) 8.7 mm, (*D*) 8.9 mm, (*E*) 12.1 mm. Shading conventions as in Fig. 3.

groove, in albumen and capsule glands.

Material examined. 71 lots (17 AMS, 14 USNM, 13 BMNH, 2 IRSNB, 4 NMW, 21 MNZ), including 6 penes, 4 sperm samples, 4 pallial oviducts, 4 radulae.

Shell (Fig. 12). Mature shell height 8.9–20.2 mm. Shape high-turbinate to tall-spired, occasionally patulous or globular (H/B = (1.11)1.29–1.79; SH = (1.26)1.47–2.34); spire outline straight; whorls rounded, suture impressed, periphery slightly angled; solid. Columella pillar straight or slightly concave; columella excavated; eroded parietal area usually present. Sculpture of 8–12 approximately equidistant primary spiral grooves (incised lines) above periphery, continuing on base; grooves occasionally obsolete; rarely, ribs between grooves become raised and prominent at periphery; microstriae faint or absent; surface, especially spire, often eroded; growth lines weak. Protoconch rarely preserved, about 3 whorls, 375–425 μm length, sculptured by spiral rows of minute tubercles (Pilkington, 1971). Colour cream with pale to dark brown spiral lines (corresponding to spaces between grooves); rarely, lines are faint or narrow (Fig. 12F); occasionally entirely brown with pale grooves on base only; occasionally cream with a broad peripheral brown band and few spiral brown lines on base (Fig. 12D); juveniles black or brown with one or more spiral white lines on base; aperture dark brown with basal white band.

Animal. Head, tentacles and sides of foot black. Opercular ratio 0.44–0.54. Penis (Fig. 13A–D): filament 0.5 total length of penis, smooth or slightly wrinkled, bluntly pointed, slightly swollen, reddish coloration at base of filament when live; sperm groove opens terminally; single mamilliform gland and adjacent large flap of penial glandular disc borne together on broad lateral branch of base; penial base often with black pigment. Euspermatozoa 79–86 µm; paraspermatozoa (Fig. 13G,H) spherical, 10–13 µm diameter, containing large spherical granules and a curved, twisted or torus-shaped rod body. Pallial oviduct (Fig. 13E) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, within which portion adjacent to egg groove (translucent capsule gland) is differentiated as a ring; copulatory bursa large, opening near anterior end of straight section, extending back beneath capsule gland.

Spawn and development. Spawn (Fig. 13F) a transparent pelagic capsule 250 µm diameter, containing a single ovum 80 µm diameter, capsule with domed upper surface sculptured by 3 concentric rings, peripheral ridge and a basal circumferential flange; development planktotrophic; spawning season November to March (at Otago; Pilkington, 1971).

Radula (Fig. 4G,H). Relative radular length 3.5–5.6. Rachidian: length/width 1.18–1.30; major cusp elongate, rounded to slightly pointed at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded to slightly pointed at tip. Outer marginal: 7–9 cusps.

Habitat. This species is most abundant in the southern areas of New Zealand, where it occupies a vertical range from the littoral fringe to the barnacle zone, and may even extend to the kelp (*Durvillea*) zone (at Otago; Batham, 1958; Morton & Miller, 1968). There is some downward migration during the spawning season (Pilkington, 1971). Although its upper vertical limit is below that of the frequently sympatric *A. antipodum*, it has a wider range of habitat; it reaches further down the shore, is common in sheltered and exposed sites, and extends further into turbid bays (Batham, 1956; Morton & Miller, 1968). Further north in South Island, its tidal range is more restricted than that of *A. antipodum* and its distribution is centred on more sheltered shores than that species, being most frequent on irregular rock with numerous crevices (at Banks Peninsula; Knox, 1953). In North Island, it is sparse on the east coast of Auckland, where it is restricted to open coasts, but more common on the Auckland west coast (Morton & Miller, 1968).

Range (Fig. 14). New Zealand, Auckland Islands, Chatham Islands. This species occurs throughout the two main islands of New Zealand (northernmost record: The Bluff, Ninety-Mile Beach, 34°41'S 172°54'E, AMS C406343), on Stewart Island (Port Pegasus, 47°09'S 167°42'E, MNZ M026145), Snares Islands (Rima Islet, 48°02'S 166°38'E, MNZ M058350), Auckland Islands (Rose Island, 50°31'S 166°15'E, MNZ M155923) and Chatham Islands (Waitangi Bay, 43°57'S 176°33'W, MNZ M110471; Powell, 1933b).

Remarks. The shell shows considerable variability in both shape and colour. Shape ranges from elongate to globular or even patulous. Possible correlation with environmental variables has not been recorded but, by analogy with other species (e.g., *A. unifasciata*) the wide-mouthed forms might be found on more exposed coasts.

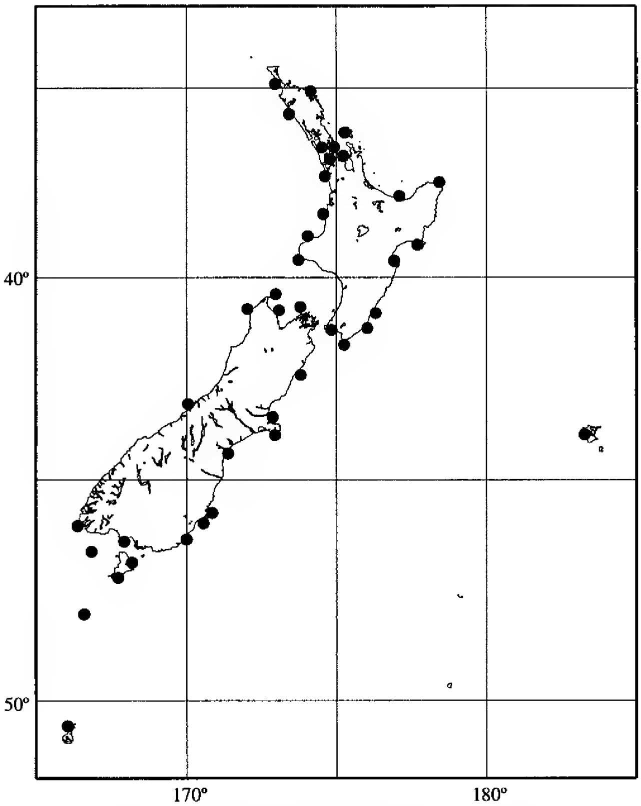

Fig. 14. Distribution of *Austrolittorina cincta*.

Of the two species of *Austrolittorina* in New Zealand, *A. cincta* has the darker coloration and more southerly (i.e. higher latitude) distribution, whereas *A. antipodum* has a paler shell and more northerly distribution. This might be an example of climatic selection, with dark, heat-absorbing shells in cooler climates. A similar case has been noted in the intraspecific variation of *A. araucana* (Reid, 2002*a*) and another in the pair *Afrolittorina africana* and *A. knysnaensis* (described below).

This species is sympatric with *A. antipodum* throughout most of its range; however, its distribution is more southern, for it is more common in the south of its range (Suter, 1913) and extends to the Auckland Islands (where *A. antipodum* does not occur). In the north it does not reach the Three Kings Islands or the Kermadec Islands, in contrast to *A. antipodum*. The two species are readily discriminated by the brown colour or lined pattern of *A. cincta*; when, rarely, the pattern is faint or reduced to a peripheral band only, the base still retains a few brown lines close to the columella, and the spiral grooves are more pronounced than in *A. antipodum*. Anatomically, there is only a slight difference in the penial shape, the filament being slightly more pointed in *A. cincta*.

Austrolittorina araucana (d'Orbigny, 1840)

Littorina araucana d'Orbigny, 1840: 393–394; Atlas pl. 53, figs. 8–10 (Valparaiso, Chili, also entire coast as far as Arica, Pérou [Valparaíso, Chile, to Arica, Chile], restricted to Valparaíso (Reid, 2002*a*); lectotype (Reid, 2002*a*) BMNH 1854.12.4.365/1; 12 paralectotypes BMNH 1854.12.4.365/2, seen).

Nodilittorina araucana Reid, 2002*a*: 142–145, figs16G, H (radula), 18A–J, 19A–C (penes), F (egg capsule), H (pallial oviduct), J, K (paraspermatozoa), 20 (distribution).
Austrolittorina araucana.—Williams *et al*., 2003.

Taxonomic history. For full synonymy see Reid (2002*a*).

Diagnosis. Shell small, periphery rounded; sculpture of numerous fine spiral grooves, becoming obsolete; white to dark brown with pale basal band. Penial filament broad, with subterminal opening of sperm groove; mamilliform gland and small glandular disc on base. Pallial oviduct with simple loop of egg groove in albumen gland followed by flexure in capsule gland.

Range. Peru to southern Chile.

Remarks. This species is highly variable in shape, and ranges from white to blue-grey or uniform brown in colour, rarely with indistinct markings. Some pale shells are close in appearance to small examples of *A. unifasciata* and *A. fernandezensis*, but the three are allopatric and the pallial oviduct and penis of *A. araucana* are unique.

Molecular data have shown this species to be the basal member of the genus. Its separation from the four other living species was estimated at 40–73 million years ago, and therefore of sufficient age to be ascribed to the fragmentation of Gondwana (Williams *et al*., 2003).

Afrolittorina Williams, Reid & Littlewood, 2003

Type species. *Litorina africana* Krauss, in Philippi, 1847.

Taxonomic history. Both *Afrolittorina africana* and *A. knysnaensis* were classified by Rosewater (1970) as members of his new subgenus *Littorina (Austrolittorina)*, on the basis of their non-nodulose shells and *Nodilittorina*-like penes and radulae. The two remaining members, *A. praetermissa* and *A. acutispira* were transferred to *L. (Austrolittorina)* subsequently (Ponder & Rosewater, 1979). These four species were included in *Nodilittorina (Austrolittorina)* by Reid (2002*a*), as defined by the loop of the egg groove through the capsule gland of the pallial oviduct. A formal cladistic analysis of morphological characters of *Nodilittorina s.l.* (Reid, 2002*b*) did not support *Austrolittorina* as a monophyletic group. However, it did identify these four species as a clade, supported by the single unequivocal and unreversed synapomorphy of the loop of the egg groove through the jelly gland (elsewhere in the subfamily this feature is found only in *Melarhaphe neritoides*, in which the loop is elaborated into a spiral). DNA-sequence data have since shown unequivocally that the four species are not members of the *Austrolittorina* clade, but are the sister group of the northern-hemisphere genus *Littorina*, thus justifying the introduction of the new genus *Afrolittorina* (Williams *et al*., 2003).

Diagnosis. Shell not nodulose; spiral striae or smooth; eroded parietal area usually absent; no pseudoumbilicus; pale with diffuse pattern of mottling, marbling or tessellation, rarely axially aligned. Cephalic tentacles with transverse lines, 1–2 longitudinal black stripes, or black. Penis with swollen filament; base bifurcate; single mamilliform gland; glandular disc of subepithelial glandular tissue may be large, minute or absent; if absent, epithelium around mamilliform gland is tall and secretory; penial vas deferens an open groove. Rod bodies of paraspermatozoa long and straight, or small and irregular. In pallial oviduct egg groove makes a simple loop through albumen gland, large circular loop through capsule gland, smaller loop in jelly gland; copulatory bursa opens in posterior position. (After Williams *et al*., 2003.)

Afrolittorina africana (Krauss, in Philippi, 1847)

Figs. 15–16, 17A,B, 18

Litorina africana Krauss, in Philippi, 1847: 199, *Litorina* pl. 4, fig. 10 (Caput Bona Spei [Cape of Good Hope, South Africa; restricted to Algoa Bay, Krauss, 1848]; lectotype (Janus, 1961) Stuttgart Museum ZI 0050275 (formerly MT 106; fig. 15A; seen) plus 1 paralectotype ZI 0050276; possible paralectotypes Senckenberg Museum SMF 314707/1 (Herbert & Warén, 1999); additional paralectotypes may be in Nationaal Natuurhistorisch Museum, Leiden [van Bruggen, 1992: 83]). Krauss, 1848: 102. Weinkauff, 1878: 37, pl. 4, figs. 5–6. Weinkauff, 1883: 218 (includes *A. knysnaensis*).
Littorina africana.—Reeve, 1857: *Littorina* sp. 37 (in part; pl. 8, fig. 37 is *L. unifasciata*). Nevill, 1885: 137. Bartsch, 1915: 120. Tomlin, 1923: 49. Dautzenberg, 1932: 60. Turton, 1932: 132, 133. Kilburn & Rippey, 1982: 50, pl. 10, fig. 1. Potter & Schleyer, 1991: pl. 2.2, 2.3 (radula).
Littorina (Melarhaphe) africana.—Adams & Adams, 1854: 314 (as *Melaraphe*). Tryon, 1887: 248–249, pl. 44, figs. 66–67 (as *Melaraphe*; in part; figs. 65, 68 are *Afrolittorina knysnaensis*; fig. 69 is *Echinolittorina quadricincta* Mühlfeld, 1824). Janus, 1961: 5 (as *Melaraphe*).
Littorina (Austrolittorina) africana.—Rosewater, 1970: 423, 476–477, pl. 364, figs. 11–16, pl. 365, fig. C (penis), pl. 368 (distribution). Kilburn, 1972: 399–401 (probably subspecies of *Austrolittorina unifasciata*).
Nodilittorina africana.—Bandel & Kadolsky, 1982: 3. Reid, 2002*b*: fig. 2a (penis).
Nodilittorina (?Echinolittorina) africana.—Reid, 1989: 99, fig. 10i (oviduct) (*A. knysnaensis* doubtfully included).
Nodilittorina (Austrolittorina) africana.—Reid, 2002*a*: 154.
Afrolittorina africana.—Williams *et al*., 2003.
Litorina decollata Krauss, in Philippi, 1847: 196; *Litorina* pl. 4, fig. 3 (Ora Natal Africae [coast of Natal, South Africa]; lectotype (Janus, 1961) Stuttgart Museum ZI 0050277 (formerly MT 107; fig. 15F; seen) plus 26 paralectotypes ZI 0050278; possible paralectotypes Senckenberg Museum SMF 314709/3 and uncatalogued (Herbert & Warén, 1999); 15 possible paralectotypes MCZ 154113; 2 paralectotypes ZMA; additional paralectotypes may be in Nationaal Natuurhistorisch Museum, Leiden [van Bruggen, 1992: 83]). Krauss, 1848: 102. Küster, 1856: 9, pl. 1, figs. 14–15. Weinkauff, 1878: 28. Weinkauff, 1883: 219 (in part; includes *A. knysnaensis*).
Littorina (Melarhaphe) decollata.—Adams & Adams, 1854: 314 (as *Melaraphe*). Janus, 1961: 5–6 (as *Melaraphe*).
Littorina decollata.—Reeve, 1858: *Littorina* sp. 92, pl. 17, fig. 92. Sowerby, 1892: 36. Turton, 1932: 132.
Littorina caerulescens.—Tenison Woods, 1879: 65–72 (as *coerulescens*; not *Turbo caerulescens* Lamarck, 1822 = *Melarhaphe neritoides*; in part; includes *Austrolittorina unifasciata*, *Austrolittorina antipodum*, *Afrolittorina praetermissa*, *Littoraria mauritiana*, *L. undulata*, *M. neritoides*).
Littorina knysnaensis.—Sowerby, 1892: 36 (not *Litorina knysnaensis* Krauss, in Philippi, 1847 = *A. knysnaensis*; in part; includes *A. knysnaensis*).
?Littorina perplexa Turton, 1932: 133, pl. 28, fig. 960 (Port Alfred, South Africa; holotype OUM, seen).

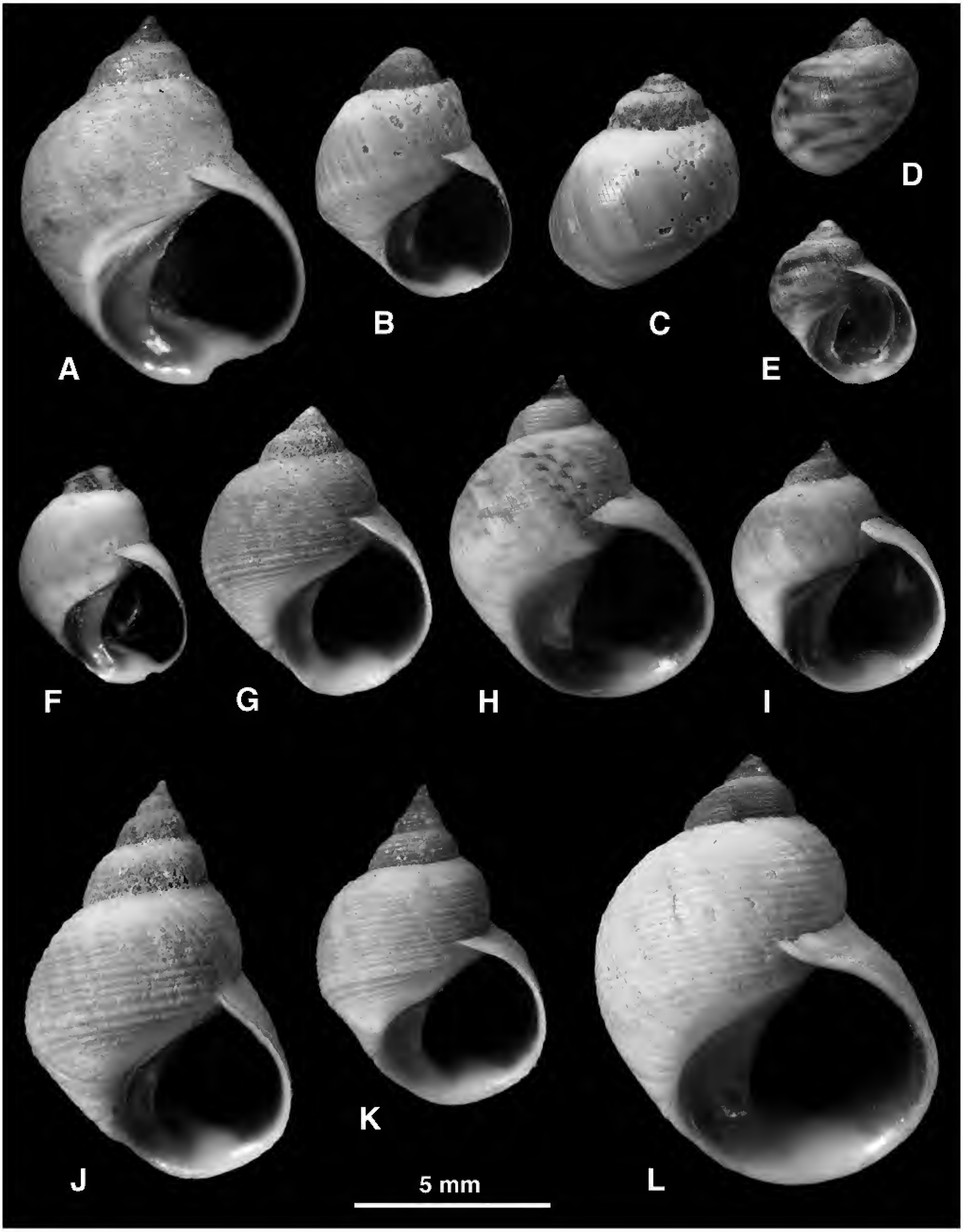

Fig. 15. *Afrolittorina africana*: (*A*) Lectotype of *Litorina africana* Krauss, in Philippi, 1847; no locality (Stuttgart Museum ZI 0050275). (*B*) Port Elizabeth, South Africa (BMNH 20030415). (*C*) Flat rock surfaces and pools, Umngazana, South Africa (BMNH 20030416). (*D,E*) Umhlanga Rocks, South Africa (BMNH 20030417). (*F*) Lectotype of *Litorina decollata* Krauss, in Philippi, 1847; no locality (Stuttgart Museum ZI 0050277). (*G,K*) Concrete wall, Umngazana, South Africa (BMNH 20030418). (*H,I,L*) Richards Bay, South Africa (BMNH 20030419). (*J*) Arniston, South Africa (BMNH 20030420).

Taxonomic history. Krauss (1848) described three new littorinids from South Africa, *Litorina africana, L. decollata* and *L. knysnaensis* but, owing to his habit of sending specimens and manuscript names to colleagues, the names and descriptions had appeared a year earlier in the monograph of *Litorina* by Philippi (1847). Krauss was credited with authorship in this earlier publication (see biographical notes on Krauss and discussion of his taxa by Herbert & Warén, 1999). Later authors maintained these taxa as distinct until the first revision by Tryon (1887), who correctly synonymized *L. decollata* with *L. africana* (thereby establishing the valid name for this species, despite the page priority of *L. decollata*). Among later authors, only Sowerby (1892), Turton (1932) and Janus (1961) have continued to regard *L. decollata* as a distinct species.

The shells of the two species are usually easily separable, so it is surprising that there has been a long history of confusion and combination of *A. africana* and *A. knysnaensis*. Weinkauff (1883) and Tryon (1887) both regarded *knysnaensis* as a variety of *L. africana*, whereas Sowerby (1892) combined both under the former name. Bartsch (1915) recognized both species, yet described elongate examples of *A. knysnaensis* as *L. africana tryphena*. Although Rosewater (1970) clearly described the characteristic shells of the two species, Hughes (1979) once again combined the two as varieties of *L. africana*. The evidence for this was that "the complete range of intermediate forms in shell colour and morphology, and the absence of differences in radulae, penial morphology or habitat suggest that these forms represent a dimorphic species showing a genetic cline correlated with latitude" (Hughes, 1979). The relative proportions of the blue-grey *A. africana* and brown *A. knysnaensis* do indeed change from 0 to 100% along the South African coast between False Bay and Natal. However, although the shell of *A. knysnaensis* can sometimes be pale in colour, the two species remain distinct in shell shape and sculpture. Most significantly, the penes are distinct, particularly in their pigmentation, as observed by Hughes himself. Subsequent authors (Kilburn, 1972; Bandel & Kadolsky, 1982) retained the two as distinct species, although Reid (1989) doubtfully synonymized them.

The identity of *Littorina perplexa*, described by Turton (1932) from Port Alfred, is puzzling. Rosewater (1970) listed it in the synonymy of "*Littorina punctata* (Gmelin, 1791)" (presently interpreted as a complex of three species, including *Echinolittorina punctata*; Reid, 2002*b*). Noting that *E. punctata s.l.* does not occur in South Africa, Kilburn (1972) interpreted *L. perplexa* as a form of *A. africana* with a patterned shell. The unique holotype is a beachworn shell 1.9 mm in height, of about two teleoconch whorls, with a low-turbinate shape, weak spiral grooves, eroded apex and well-developed tessellated pattern. At this small size none of the three turbinate littorinids recorded from Port Alfred (*A. africana, A. knysnaensis, Littoraria intermedia* [Philippi, 1846]) has been seen to develop a distinct tessellated pattern of this kind, so although Kilburn's attribution is possible, it can be doubted. The shell does indeed resemble a juvenile specimen of the *E. punctata* complex, perhaps accidentally transported to Port Alfred.

Reeve (1857) inadvertently described and figured a shell of *Austrolittorina unifasciata* as *Littorina africana*, as noted by Smith (1884, as *L. mauritiana*). The South African species has occasionally been united with species of *Austrolittorina* as a single taxon (Tenison Woods, 1879; see Taxonomic History of *Austrolittorina unifasciata*). Kilburn (1972) revived this idea, suggesting that *Littorina africana* might prove to be a subspecies of *Littorina unifasciata*, a circumpolar taxon.

Diagnosis. Shell small, turbinate, usually sculptured with fine spiral threads; white with broad blue-grey band above periphery, sometimes with additional fine, pale brown tessellation. Penis with bluntly blade-shaped, red-brown (greyish black when preserved) filament; mamilliform gland on base, but no glandular disc. Pallial oviduct with three consecutive loops of egg groove, in albumen gland, capsule gland and in terminal portion of oviduct.

Material examined. 52 lots (6 AMS, 3 USNM, 38 BMNH, 1 IRSNB, 1 ZMA, 1 MNHNP, 2 NM), including 16 penes, 3 sperm samples, 16 pallial oviducts, 6 radulae.

Shell (Fig. 15). Mature shell height 3.7–12.0 mm (13.5 mm, Rosewater, 1970). Shape globular to turbinate (H/B = 1.20–1.66; SH = 1.18–1.91); spire outline slightly concave at apex; whorls well rounded, suture distinct, periphery rounded or slightly angled; moderately solid. Columella pillar straight to slightly concave; columella broad, slightly excavated; eroded parietal area usually absent but may be present in low-spired shells. Sculpture of numerous fine spiral threads and striae (not clearly differentiated into primary grooves, ribs and microstriae); on early teleoconch whorls 8–11 threads visible above suture, with striae between; on last whorl numerous closely spaced coarse striae over entire whorl, of which 15–27 may be raised as narrow cords; periphery not marked by an enlarged rib; sometimes almost smooth with only faint spiral striae; growth lines may be present towards end of last whorl; spire often eroded. Protoconch rarely preserved, about 0.34 mm diameter, 3 whorls. Colour white to cream, with broad spiral band of blue-grey from just below suture to below periphery; darker pattern may be absent, but fine tessellation of yellow or pale brown is often faintly visible over entire surface of last whorl (Fig. 15G,H); rarely, pattern is developed into conspicuous oblique, spiral or zigzag brown lines (Fig. 15D,E); eroded spire blackish brown; aperture dark brown with basal white band; first 2 whorls of teleoconch fawn.

Animal. Head and sides of foot grey to black; tentacles with fine black transverse lines (sometimes faint or absent). Opercular ratio 0.37–0.44. Penis (Fig. 16A–J): filament 0.5–0.6 total length of penis, bluntly blade-shaped and slightly swollen, coloured red brown in life (dark greyish black in preserved specimens) by subepithelial glandular tissue; sperm groove open almost to filament tip; single mamilliform gland borne on lateral branch of base; glandular disc absent; instead the epithelium around the papilla of the mamilliform gland is tall and glandular; base unpigmented. Euspermatozoa length unknown; paraspermatozoa (Fig. 16M) spherical to oval, 11–19 µm diameter, containing large spherical granules and single hexagonal or irregular rod-body, rarely projecting from cell. Pallial oviduct (Fig. 16K,L) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, of which a small distal part may be differentiated as reddish translucent capsule gland; additional simple loop of glandular material between capsule gland and terminal portion of pallial

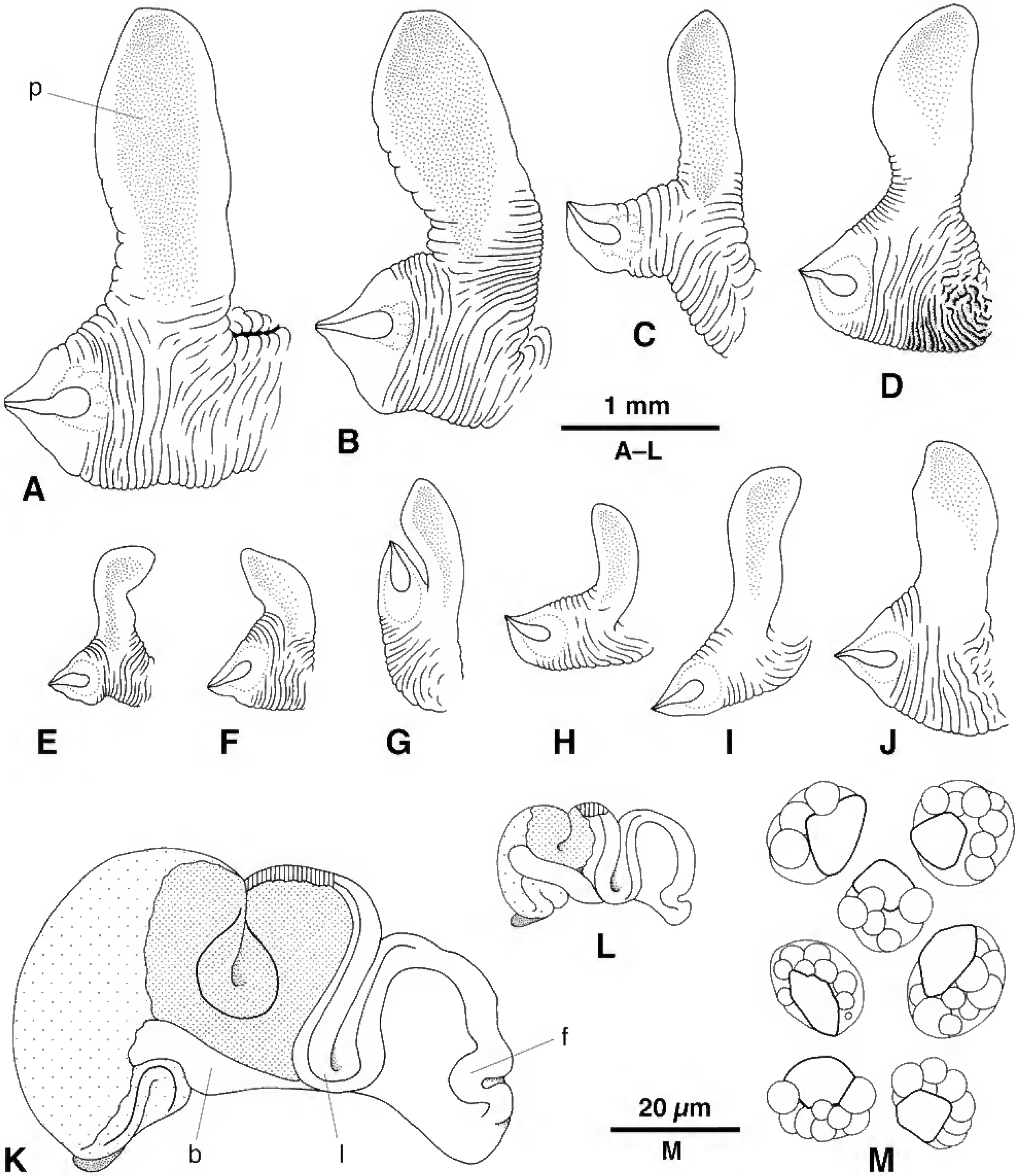

Fig. 16. *Afrolittorina africana*: (*A–J*) Penes. (*K,L*) Pallial oviducts. (*M*) Paraspermatozoa from one specimen. (*A–C,M*) Munster, South Africa (BMNH 20030412). (*E,F,L*) Umngazana, South Africa (from "*decollata*" shell form; BMNH 20030422). (*G–I*) Umhlanga Rocks, South Africa; ([*G,H*] from crevice-dwelling shell form, BMNH 20030423; [*I*] from normal shell form; BMNH 20030424). (*J*) Richards Bay, South Africa (BMNH 20030425). (*K*) Salt Rock, South Africa (BMNH 20030426). Shell heights: (*A*) 10.4 mm, (*B*) 10.5 mm, (*C*) 5.8 mm, (*D*) 6.7 mm, (*E*) 4.7 mm, (*F*) 5.4 mm, (*G*) 4.2 mm, (*H*) 3.7 mm, (*I*) 5.0 mm, (*J*) 8.2 mm, (*K*) 10.2 mm, (*L*) 5.2 mm. Abbreviations: (*b*) copulatory bursa; (*f*) terminal flexure of egg groove; (*l*) loop of egg groove between capsule gland and straight section of pallial oviduct; (*p*) dark pigment of subepithelial glandular tissue visible by transparency in penial filament. Shading conventions as in Fig. 3.

oviduct; small flexure of egg groove just before opening to mantle cavity; large copulatory bursa separates in a posterior position and continues back to overly capsule gland.

Spawn and development. Not recorded; pelagic spawn and planktotrophic development predicted from dimensions of protoconch and large capsule gland (Reid, 1989).

Radula (Fig. 17A,B). Relative radular length 4.1–7.6 (4.03, s.e. 0.33; Potter & Schleyer, 1991). Rachidian: length/width

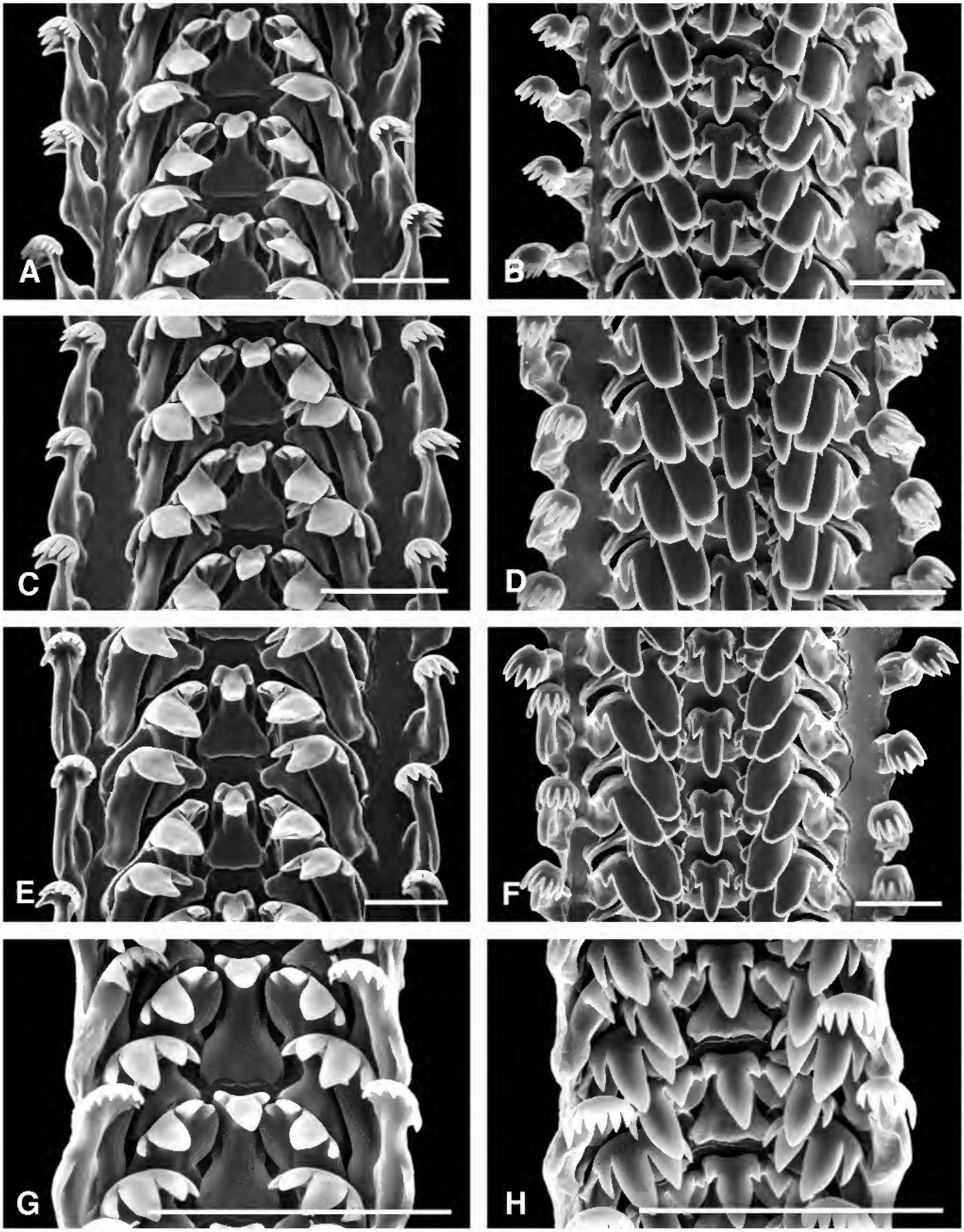

Fig. 17. Radulae; views of same specimen flat (*A,C,E,G*) and at 45° from anterior end (*B,D,F,H*). (*A,B*) *Afrolittorina africana*, Salt Rock, South Africa (BMNH 20030426; shell H = 10.2 mm). (*C,D*) *Afrolittorina knysnaensis*, Cape Agulhas, South Africa (BMNH 20030427; shell H = 9.3 mm). (*E,F*) *Afrolittorina praetermissa*, Port Campbell, Victoria, Australia (AMS C388111; shell H = 8.5 mm). (*G,H*) *Afrolittorina acutispira*, North Harbour, Sydney, NSW, Australia (BMNH 20030446; shell H = 3.9 mm). Scale bars = 50 µm.

1.19–1.48; major cusp elongate, rounded to pointed at tip. Lateral and inner marginal: major cusps large, elongate, bluntly rounded to truncate at tip. Outer marginal: 8–10 cusps (10–11; Potter & Schleyer, 1991).

Habitat. *Afrolittorina africana* dominates the upper shore on open coasts in the Transkei and Natal, reaching densities of up to 6000 m^{-2} in the upper barnacle zone (Dye, 1988). The vertical tidal range is wide, from mean low water of neap tide to the littoral fringe; recruitment occurs on the horizontal platforms of the lower shore and is followed by upward migration (Eyre & Stephenson, 1938; Potter, 1987; Potter & Schleyer, 1991). In Natal, the northern part of the range, the vertical distribution is shifted lower on the shore, perhaps as an effect of higher temperatures (Kilburn & Rippey, 1982; McQuaid & Sherman, 1988; McQuaid, 1992). At East London, where both *A. africana* and *A. knysnaensis* are common, the former dominates in the lower parts of the littorinid zone and extends slightly lower on the shore (Eyre *et al.*, 1938). Although most abundant a range of rocky substrates on open coasts, the species can also be found in sheltered estuaries and on wooden posts (Kilburn, 1972). Juveniles feed on bacteria and diatoms, and adults mainly on lichens and blue-green algae (Potter & Schleyer, 1991).

Range (Fig. 18). southwestern Indian Ocean from near Cape Town to Natal, southern Mozambique and southeastern Madagascar. The range limits in South Africa are St James, False Bay (34°07'S 18°27'E, BMNH 20030448; Eyre, 1939) and Cape Vidal, Natal (28°08'S 32°33'E, BMNH 20030449), but the species is relatively uncommon (in comparison with the sympatric *A. knysnaensis*) further south and east than Port St Johns (31°38'S 29°33'E; Hughes, 1979), and becomes rare at Cape Agulhas (Stephenson, 1944). To the north of Cape Vidal there is a long stretch of unsuitable sandy coastline, but there are three records from southern Mozambique: Inhaca Island (26°02'S 32°58'S USNM 637363); Tofo (23°51'S 35°33'E, AMS); Morrungulo, near Massinga (23°15'S 35°22'E, NM G4627). The species just reaches southeastern Madagascar, where it is recorded from Ambovombe, (25°11'S 46°05'E, IRSNB) and Flacourt, Fort Dauphin (25°02'S 47°00'E, USNM 678834).

Remarks. This species is variable in shell characters and at least three intergrading forms can be recognized (see Kilburn, 1972, for discussion). The typical form is the largest, a turbinate shell with sculpture varying from incised lines to raised threads (Fig. 16A,G–L). The colour is white with a broad blue-grey band from below the suture to below the periphery. In the northern part of the range (at Port St Johns, in Natal and Mozambique) this may be overlain by a faint, fine, tessellated pattern of yellow or pale brown (Fig. 16G–I,K). The form described by Krauss as *Litorina decollata* is a small, low-spired shell with smooth surface, white with a broad blue-grey band, but no patterning (Fig. 16B,C,F). Kilburn (1972) noted that the *decollata* form occurred both sporadically among populations of the typical form and in pure populations, and that its occurrence was not correlated with degree of wave exposure. In BMNH two collections from the same locality, Umngazana, suggest a different correlation. A sample from concrete walls (BMNH 20030418) at this open-coast locality is of the typical form, whereas a sample from flat surfaces and pools (BMNH 20030416) is of the *decollata* form. In members of the *Echinolittorina aspera* species group from the eastern Pacific, individuals in pools at the top of the eulittoral zone are stunted and more smooth than those on rocks in the littoral fringe (Reid, 2002*a*). Stunted individuals in pools have also been noted in *Littoraria pintado pullata*

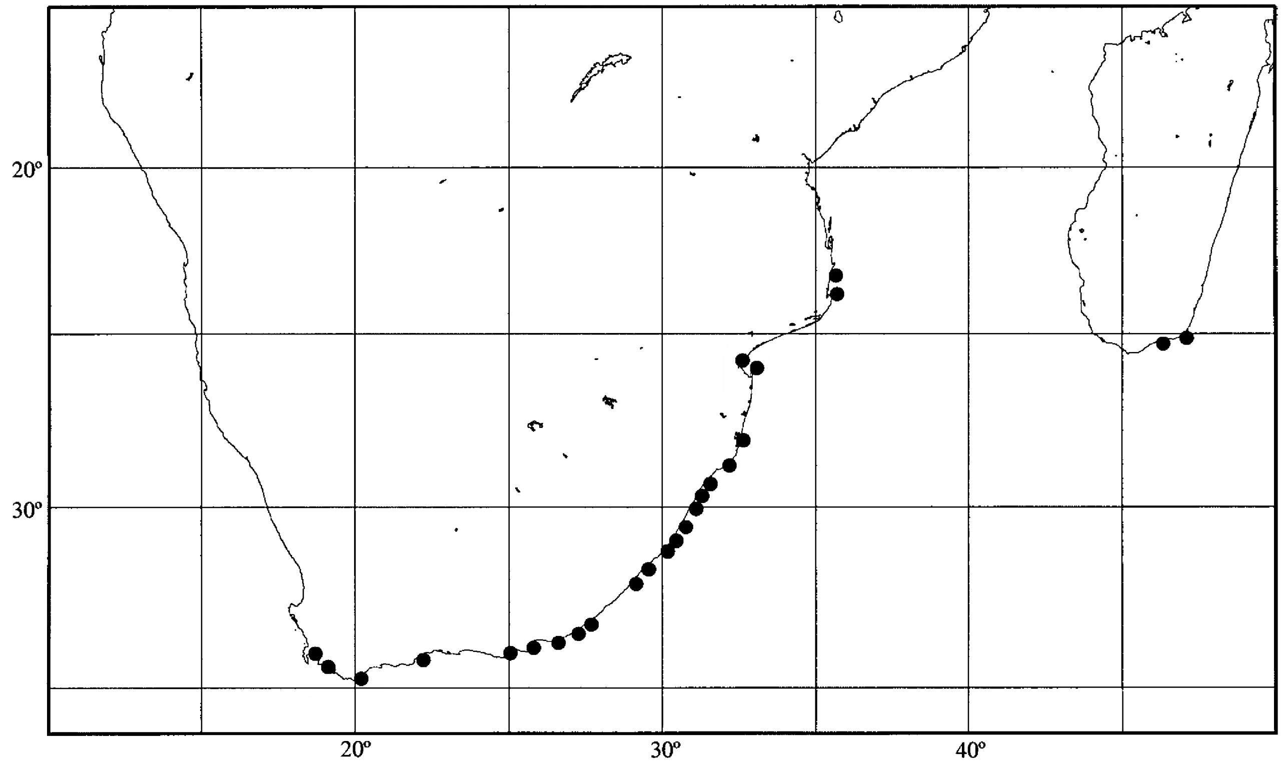

Fig. 18. Distribution of *Afrolittorina africana*.

(Carpenter, 1864) (Reid, 1999). In both these cases, as in *A. africana*, the species has planktotrophic development, so that genotypic differentiation between the shell forms is unlikely and an ecophenotypic effect may explain this pattern of small-scale variation.

Another distinctive form with a strong pattern of brown spiral lines, zigzags and coarse tessellation was mentioned by both Kilburn (1972) and Hughes (1979). Specimens collected by Hughes at Umhlanga Rocks, Natal, are small (less than 5 mm), smooth, low-spired and of patulous shape (Fig. 16D,E; BMNH 20030423). These were found in crevices and contrasted with the common typical form at the same locality (BMNH 20030424). The dimorphism of the shells at this locality is so striking that a pair of sympatric species might be suspected, yet no anatomical differences could be detected in the present study (Fig. 16G–I). Hughes (1979) pointed out the parallel with the "*neglecta*" ecotype of *Littorina saxatilis* (Olivi, 1792) (equivalent to the "barnacle ecotype" of Reid, 1996). The interpretation of these specimens as an ecophenotype of *A. africana* is supported by the finding of identical sequences of the 12S mitochondrial gene in both (S.T. Williams, unpublished).

Distinction from the partially sympatric *A. knysnaensis* is described in the Remarks on that species.

Phylogenetic analysis of morphological characters identified *A. africana* and *A. knysnaensis* as sister species on the basis of the tall, secretory epithelium surrounding the mamilliform penial gland (which may serve the function of the absent subepithelial glandular disc), and this is a unique synapomorphy (Reid, 2002*b*). This relationship was supported by DNA-sequence analysis that estimated that the two species may have diverged more than 10 million years ago (Williams *et al*., 2003). These two are in turn the sister group of the pair of Australian members of *Afrolittorina*, and the divergence time between the African and Australian pairs was estimated as 29–55 million years.

Afrolittorina knysnaensis (Krauss, in Philippi, 1847)

Figs. 17C,D, 19–21

Litorina knysnaensis Krauss, in Philippi, 1847: 196, *Litorina* pl. 4, fig. 4 (Caput Bona Spei ad regionem fluminis Knysna [Cape of Good Hope near Knysna River, South Africa]; lectotype (Janus, 1961) Stuttgart Museum ZI 0050273 (formerly MT 108; fig. 19A; seen) plus 30 paralectotypes ZI 0050274; 20 paralectotypes MCZ 154114; possible paralectotypes Senckenberg Museum uncatalogued (Knysna Fluss) and SMF 314706/7 (Algoa Bay) (Herbert & Warén, 1999); additional paralectotypes may be in Nationaal Natuurhistorisch Museum, Leiden (van Bruggen, 1992). Krauss, 1848: 102. Weinkauff, 1882: 71–72, pl. 9, figs. 10–11.

Littorina (Melarhaphe) knysnaensis.—Adams & Adams, 1854: 314 (as *Melaraphe*). Janus, 1961: 6 (as *Melaraphe*).

Littorina knysnaensis.—Reeve, 1857: *Littorina* sp. 75, pl. 14, fig. 75a,b. Troschel, 1858: 134 (radula) (as *knysnaniensis*). Sowerby, 1892: 36 (in part; includes *A. africana*). Bartsch, 1915: 120. Turton, 1932: 132, pl. 28, fig. 955. Kilburn & Rippey, 1982: 50, pl. 10, fig. 2. Potter & Schleyer, 1991: pl. 2.1 (radula).

Littorina (Melarhaphe) africana var. *knysnaensis*.—Tryon, 1887: 249, pl. 44, figs. 65, 68 (as *Melaraphe*).

Littorina (Austrolittorina) knysnaensis.—Rosewater, 1970: 423, 478–479, pl. 364, figs. 17–23, pl. 365, fig. D (penis), pl. 369 (distribution). Kilburn, 1972: 402.

Nodilittorina (Nodilittorina) knysnaensis.—Bandel & Kadolsky, 1982: 37–38.

Nodilittorina (Austrolittorina) knysnaensis.—Reid, 2002*a*: 154.

Afrolittorina knysnaensis.—Williams *et al*., 2003.

Littorina picea Reeve, 1857: *Littorina* sp. 83, pl. 15, fig. 83 (no locality; type locality designated as South Africa (Rosewater, 1970); holotype BMNH 1968320, seen).

Litorina africana.—Weinkauff, 1883: 218 (not Krauss, in Philippi, 1847; in part; includes *A. africana*).

Litorina decollata.—Weinkauff, 1883: 219 (not Krauss, in Philippi, 1847 = *A. africana*; in part; includes *A. africana*).

Littorina africana tryphena Bartsch, 1915: 120, pl. 38, fig. 6 (Port Alfred, South Africa; holotype USNM 187091, seen; paratype USNM 664353, not seen [Rosewater, 1970]).

Littorina tryphena.—Turton, 1932: 132.

Littorina rietensis Turton, 1932: 131, pl. 28, fig. 948 (Port Alfred, South Africa; holotype OUM, seen).

Littorina mauritiana acuta.—Turton, 1932: 131, pl. 28, fig. 950 (not *Litorina acuta* Menke, 1843 = *A. unifasciata*).

Littorina kowiensis Turton, 1932: 132, pl. 28, figs. 956 (Port Alfred, South Africa; 5 syntypes OUM, seen).

Littorina africana pica "Reeve" Turton, 1932: 133 (unjustified emendation of *L. picea* Reeve, 1857).

Littorina indistincta Turton, 1932: 133, pl. 28, fig. 959 (Port Alfred, South Africa; 2 syntypes OUM, seen).

Littorina punctata.—Penrith & Kensley, 1970a: 191–239 (not *Turbo punctatus* Gmelin, 1791 = *Echinolittorina punctata*). Penrith & Kensley, 1970b: 243–268 (in part, includes *E. punctata*, see Kilburn, 1972; personal observation of voucher material in SAM).

Taxonomic history. Although recognized as a distinct species by most authors throughout its history, there has been a recurring tendency to synonymize it with the sympatric *A. africana* (Weinkauff, 1883; Tryon, 1887; Sowerby, 1892; Hughes, 1979; see Taxonomic History of *A. africana*).

Reeve (1857) named a small, unlocalized shell of this species as *Littorina picea*; this was erroneously synonymized with *Litorina decollata* (= *A. africana*) by Weinkauff (1883), but correctly identified as *L. knysnaensis* by Tryon (1887). There has been confusion about the identification of the holotype of this taxon. Reeve (1857) referred to a single shell, but Rosewater (1970) incorrectly selected a "lectotype" from among "3 syntypes". An original label records that the two additional shells were added in 1877 (BMNH 1877.4.30.1, obtained from Sowerby). Rosewater (1970: 479, pl. 364, figs. 19–20) selected and figured the best specimen as "lectotype", but this is not in fact Reeve's holotype. One of the remaining two shells is a small, eroded, specimen of *A. knysnaensis* that is blackish brown above the periphery, paler near the suture and shows traces of the characteristic speckled pattern only on the base. This shell exactly matches Reeve's original figure in its pattern of erosion and growth lines, and corresponds with his description of a plain black shell with a slightly rugose surface; it is clearly the holotype.

Various unusual forms of this species have been named. *Littorina africana tryphena* Bartsch, 1915 was based on two beach-worn shells of unusually high-spired, pupoidal shape; similar specimens have been found to contain trematode parasites (see Remarks below). Turton (1932) named several small or beach-worn shells: *Littorina rietensis* is a rare form with carinate ribs; *L. kowiensis* is brown without the normal speckled pattern; *L. indistincta* was based on small brown juveniles about 2 mm tall that are probably of this species.

Bandel & Kadolsky (1982) doubtfully listed *Turbo dispar* Montagu, 1815, described from Poole, England, in the synonymy of *A. knysnaensis*, but recommended that it

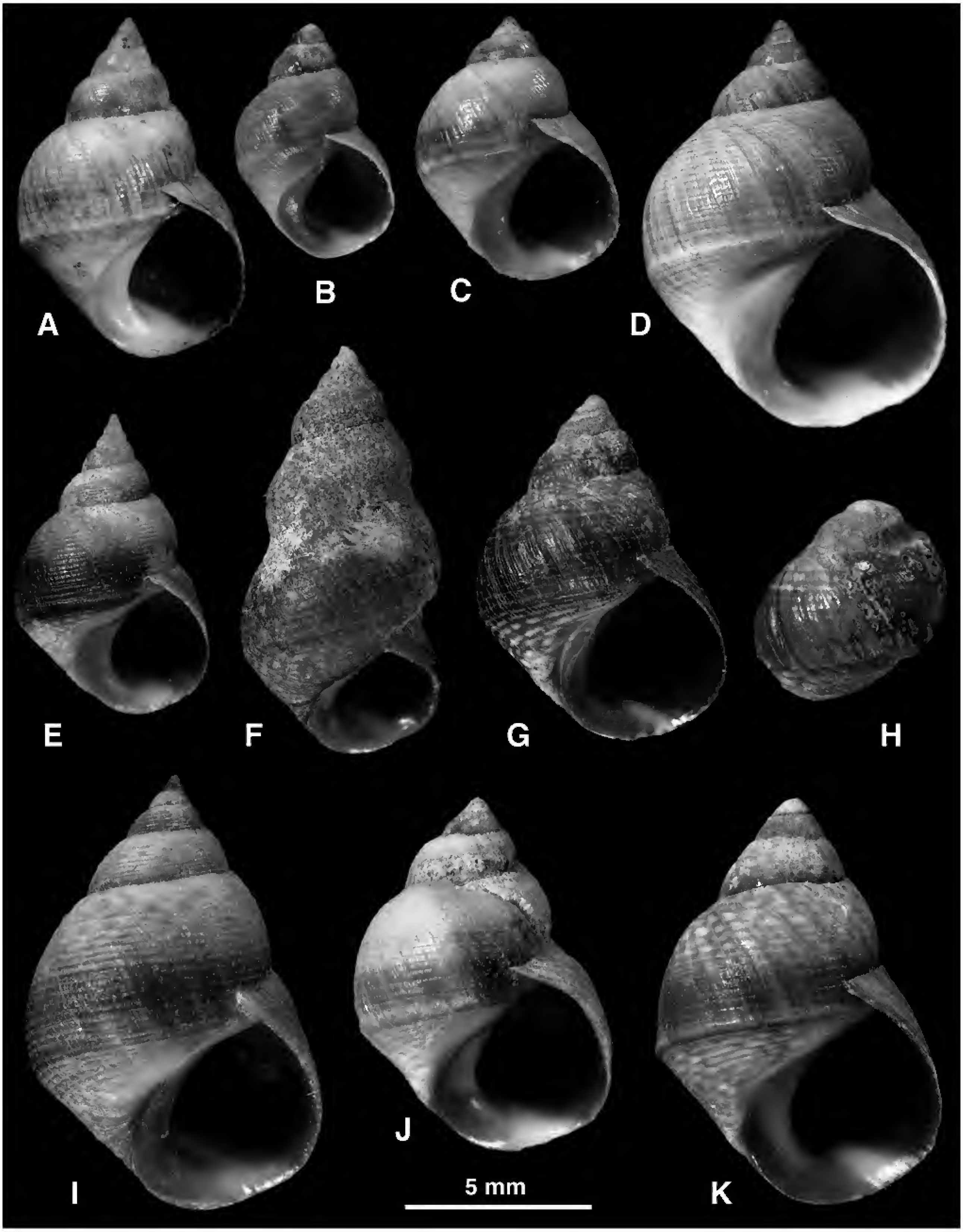

Fig. 19. *Afrolittorina knysnaensis*: (*A*) lectotype of *Litorina knysnaensis* Krauss, in Philippi, 1847; no locality (Stuttgart Museum ZI 0050273). (*B,C*) Brent, South Africa (BMNH 20030428). (*D*) Hermanus, South Africa (BMNH 20030429). (*E*) Umngazana, South Africa (BMNH 20030430). (*F,I–K*) Arniston, South Africa (BMNH 20030431). (*G*) Walvis Bay, Namibia (BMNH 20030433). (*H*) Lüderitz, Namibia (SAM A31286).

should be considered a forgotten name. Nevertheless, this can be recognized as *Melarhaphe neritoides* from the original figure and description ("obsoletely striated in a spiral direction" Montagu, 1815; not "spiral furrows", Bandel & Kadolsky, 1982), as confirmed by a specimen from Montagu's collection in the Royal Albert Memorial Museum, Exeter, England (no. 4202).

Schniebs (2000) identified the holotype of *Phasianella tesselata* Anton, 1838 as *Littorina knysnaensis*, but examination has shown this to be *Echinolittorina punctata* s.st.

Diagnosis. Shell moderately large, high-turbinate, angled at periphery, usually sculptured with fine spiral striae; pale, with fine red-brown speckling and broad bark brown band above periphery. Penis with rounded, slightly swollen filament, slight grey subepithelial glandular tissue distally, crimped lips of sperm groove; mamilliform gland on base, but no glandular disc. Pallial oviduct with three consecutive loops of egg groove, in albumen gland, capsule gland and in terminal portion of oviduct.

Material examined. 71 lots (7 AMS, 41 BMNH, 1 IRSNB, 8 ZMA, 1 MNHNP, 7 NM, 6 SAM), including 22 penes, 3 sperm samples, 11 pallial oviducts, 5 radulae.

Shell (Fig. 19). Mature shell height 3.8–19.2 mm. Shape high-turbinate (H/B = 1.26–1.61; SH = 1.29–1.92; exceptionally tall-spired specimens contain trematode parasites, H/B = 1.98, SH = 2.36; some eroded shells can appear almost globular, H/B = 1.10, SH = 1.41); spire outline slightly concave at apex; whorls moderately rounded, suture distinct, periphery angled, sharply so in juveniles, but sometimes rounded; moderately solid. Columella pillar slightly concave; columella broad, slightly excavated; eroded parietal area absent. Sculpture of numerous fine spiral elements (usually not clearly differentiated into primary grooves, ribs and microstriae); on penultimate whorl 10–13 threads visible above suture; on last whorl numerous closely spaced flat striae over entire whorl, of which 20–27 may be raised as threads; periphery marked by an enlarged riblet; occasionally almost smooth with only faint impressed spiral lines and microstriae; growth lines weak; spire often eroded. Protoconch rarely preserved, 0.34–0.43 mm diameter, 3 whorls. Colour variable, from pale grey to almost black; most commonly grey to cream ground colour, with fine red-brown speckling, palest on base, but darkening to form a broad, almost solid, brown to black band at and above periphery; palest shells grey to white, with only faint brown speckling or fine spiral lines, rarely unpatterned; darkest shells black with white speckling on base; aperture dark brown with basal white band; first 2 whorls of teleoconch brown.

Animal. Head and sides of foot grey to black; tentacles with fine black transverse lines (sometimes faint or absent). Opercular ratio 0.51–0.62. Penis (Fig. 20A–G): filament about 0.5 total length of penis, wrinkled and therefore not clearly differentiated from base, rounded and slightly expanded distally, slightly swollen, small patch of grey subepithelial glandular tissue may be visible distally; sperm groove open to filament tip, lips of groove crimped near tip; single mamilliform gland (rarely 2) borne on lateral branch of base; glandular disc absent; instead the epithelium around the papilla of the mamilliform gland is tall and glandular; base may be slightly pigmented. Euspermatozoa length unknown; paraspermatozoa (Fig. 20I) oval, 14–21 µm long, containing large spherical granules and single elongate, straight, blunt-ended rod-body 24–48 µm long projecting from cell. Pallial oviduct (Fig. 20H; not as illustrated by Gosliner, 1981) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, of which a small distal part may be differentiated as reddish translucent capsule gland; additional simple loop of glandular material between capsule gland and terminal portion of pallial oviduct; small flexure of egg groove just before opening to mantle cavity; large copulatory bursa separates in a posterior position and continues back to overly capsule gland.

Spawn and development. Not recorded; pelagic spawn and planktotrophic development predicted from egg size (87 µm, McQuaid, 1981a), from dimensions of protoconch and large capsule gland (Reid, 1989) and from low genetic differentiation on a geographical scale (Grant & Lang, 1991); continuous recruitment recorded at False Bay (McQuaid, 1981a).

Radula (Fig. 17C,D). Relative radular length 3.2–5.7 (5.59, s.e. 0.27; Potter & Schleyer, 1991). Rachidian: length/width 1.00–1.27; major cusp elongate to rectangular, bluntly rounded at tip. Lateral and inner marginal: major cusps large, elongate to rectangular, truncate at tip. Outer marginal: 7–9 cusps.

Habitat. On the rocky coasts of Namibia and South Africa (south of the Transkei) this is a dominant species on the upper shore. It is abundant across a wide zone from the littoral fringe down to the barnacle belt, extending to mean low water of neap tides (Stephenson *et al*., 1937; Bokenham *et al*., 1938; Bright, 1938; Stephenson *et al*., 1940; Penrith & Kensley, 1970a,b, as *Littorina punctata*; Kensley & Penrith, 1980; McQuaid, 1981a, 1992). The vertical range is less wide on shores of moderate exposure, and the species is absent from sheltered and muddy bays (Penrith & Kensley, 1970a, as *Littorina punctata*). Settlement occurs mainly at the top of the shore, to avoid heavy wave action, although some settlement also takes place in crevices at lower levels; adults move downwards as they grow, to reach more abundant food (McQuaid, 1981b). Where both species occur, *A. knysnaensis* and *A. africana* show broad overlap of their vertical ranges (Hughes, 1979), although at East London the former has a higher vertical limit (Eyre *et al*., 1938). The temperature relations of these two species differ, *A. knysnaensis* attaining higher tissue temperatures when attached by mucus in full sun, as a consequence of its darker coloration; it therefore occurs mainly in shaded microhabitats (McQuaid & Scherman, 1988).

Range (Fig. 21). Namibia and South Africa. On the Atlantic coast the northernmost samples examined are from Honolulu (20°36'S SAM A31185) and Rocky Point (18°59'S SAM A31184) (as also recorded by Kilburn, 1972). On the Natal coast the northernmost records are one specimen from Umhlali (29°20'S 31°14'E, Stephenson, 1947), one shell from Amanzimtoti (30°03'S 30°53'E, BMNH) and another from Umkomaas (30°12'S 30°48'E, NM 8604; also Kilburn, 1972), but the species is relatively uncommon (in comparison with the sympatric *A. africana*) to the north of Port St Johns (31°38'S 29°33'E; Hughes, 1979, also Stephenson, 1944).

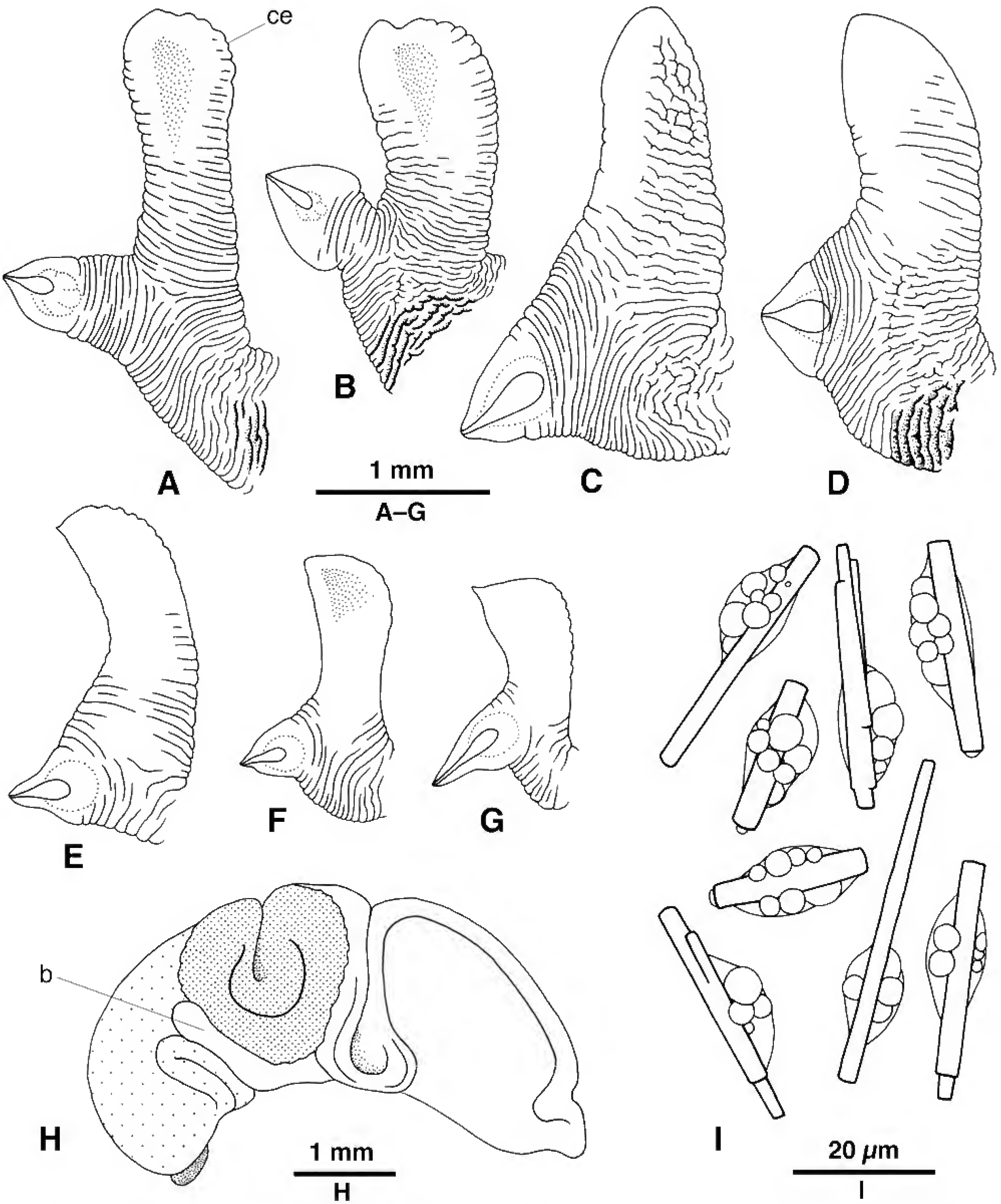

Fig. 20. *Afrolittorina knysnaensis*: (*A–G*) Penes. (*H*) Pallial oviduct. (*I*) Paraspermatozoa from one specimen. (*A,B,I*) Munster, South Africa (BMNH 20030434). (*C,D,H*) Oudekraal, South Africa (BMNH 20030435). (*E*) Knysna Head, South Africa (BMNH 20030436). (*F*) Port Edward, South Africa (BMNH 20030437). (*G*) Brent, South Africa (BMNH 20030438). Shell heights: (*A*) 6.5 mm, (*B*) 10.1 mm, (*C,D*) unknown, (*E*) 8.1 mm, (*F*) 6.5 mm, (*G*) 5.7 mm, (*H*) 14.9 mm. Abbreviations: (*b*) copulatory bursa; (*ce*) crimped edge of penial sperm groove. Shading conventions as in Fig. 3.

Remarks. Although they have been synonymized by several authors, the shells of *A. knysnaensis* and *A. africana* are almost always immediately separable by their coloration. That of *A. africana* is blue-grey, sometimes with faint fine tessellation of yellow-brown; that of *A. knysnaensis* is densely and minutely speckled with red-brown, with a broad blackish peripheral band. Occasional pale or unpatterned shells of *A. knysnaensis* are more difficult to identify, but the periphery is usually more strongly angled than in *A. africana*. The operculum is more tightly wound in *A. knysnaensis* (i.e. higher opercular ratio). Anatomically, the penial filament of *A. knysnaensis* is more wrinkled, with a

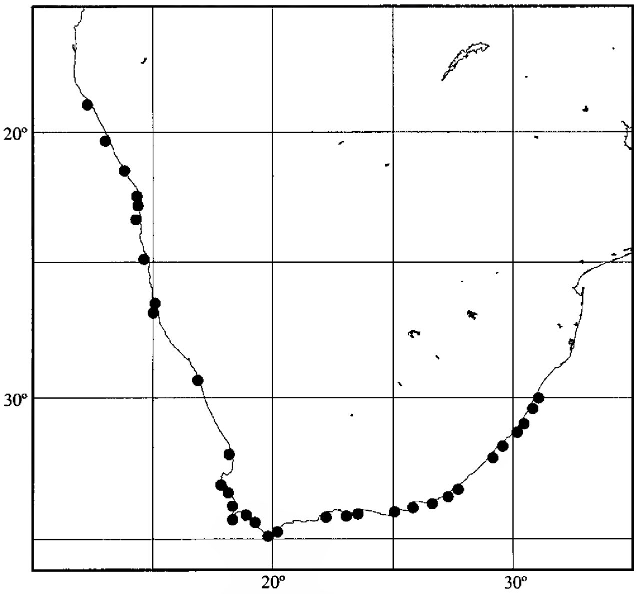

Fig. 21. Distribution of *Afrolittorina knysnaensis*.

crimped margin to the distal part of the sperm groove, the grey colour of the subepithelial glandular tissue within the filament is slight or absent, and the rod-bodies within the paraspermatozoa are much longer and project from the cells. No anatomical difference has been detected between the females of the two species. Both Rosewater (1970) and Hughes (1979) have noted that the margin of the mantle is pigmented in *A. africana* and not in *A. knysnaensis*, but this character is inconsistent and both pigmented and unpigmented states can be found frequently in both species.

Distribution maps give the impression of a broad overlap between the ranges of *A. knysnaensis* and *A. africana*, from False Bay to the vicinity of Durban. However, in a survey of the distribution of these species on the South African coast, Hughes (1979) found that *A. knysnaensis* was dominant at all sites as far north as East London, both species were common at Port St Johns, and only *A. africana* was common in Natal. *Afrolittorina knysnaensis* occurs alone on the Atlantic coast of southern Africa, under the influence of the cold Benguela Current, and is clearly a cool-temperate species, whereas *A. africana* shows a warm-temperate and subtropical distribution (Stephenson, 1944). The temperature relations of these two species have been studied by McQuaid & Scherman (1988), who showed that body temperatures of brown-shelled *A. knysnaensis* were 2–3°C higher than those of white-shelled *A. africana*, when both were attached by mucus to open rock surfaces on the shore in full sunlight (there was no difference when attached by the foot, because conductive heat gain overrode the effect of decreased radiant absorption by the paler shell). Behavioural observations also showed that *A. knysnaensis* was less tolerant of insolation than *A. africana*, for the former tended to occur in damp, shady pits in the rock rather than on open surfaces, at least when subjected to long periods of emersion during neap tides. These authors suggested that the lower tolerance of *A. knysnaensis* to heating by sunlight might explain its replacement by *A. africana* on the subtropical east coast of South Africa. There is an interesting parallel with the two species of *Austrolittorina* in New Zealand, where the brown *A. cincta* is more common in the south and the blue-white *A. antipodum* in the north. In Australia, *Afrolittorina praetermissa* has a patterned or brown shell and is a cool-water species, whereas *Austrolittorina unifasciata* with a white shell extends along warm-temperate coasts. The pattern is repeated within *Austrolittorina araucana* on the west coast of South America, where entirely brown populations occur in the south and mixed brown and white populations in the north (Reid, 2002*a*). Climatic selection might account for all these trends. The importance of pale shells as a means of temperature regulation in intertidal gastropods has been reviewed by Vermeij (1973) and has also been recorded in some tropical littorinid species (Markel, 1971). McQuaid & Scherman (1988) found no evidence of visual selection on shell colour, but Hughes (1979) noted a correlation between the abundance of *Afrolittorina africana* and pale rocks, implying that visual selection might also be involved.

Two other littorinid species have been recorded from the temperate coast of southern Africa. *Littorina saxatilis* (Olivi, 1792) occurs at two sites, Langebaan and Knysna, among marsh grass and on stones in sheltered lagoons. Neither of the southern African *Afrolittorina* species can be found in this habitat. The shells of these populations of *L. saxatilis* are smooth, thin-walled, with well-rounded whorls and are variously coloured in shades of yellow and brown, usually with a coarsely marbled or tessellated pattern. Anatomically they are quite distinct and no confusion should occur (see Reid, 1996, for review). These colonies are apparently the basis for the records of "*Littorina punctata*" in South Africa by Barnard (1963; see Kilburn, 1972). Rosewater (1970) accepted Barnard's records of "*L. punctata*" from South Africa and added others from Port Elizabeth; these may have been based on misidentification of *A. knysnaensis*, for *E. punctata* does not occur south of Namibia (Kilburn, 1972). It has recently been suggested that *Echinolittorina punctata* consists of a complex of three species (Reid, 2002*b*), of which the one in Namibia should be known as *Echinolittorina pulchella* (Dunker, 1845). Kilburn (1972) stated that the range of this species abuts that of *A. knysnaensis* at Rocky Point in Namibia, where both species occur together. Furthermore, he suggested that the presence of apparent intermediates (in shell pattern) to the south implied hybridization. It is true that shells of *E. pulchella* and of *A. knysnaensis* can be similar, but it is now clear that there are significant anatomical differences between the two. The pallial oviduct of *E. pulchella* contains only a single loop of the egg groove, in the albumen gland, and the penis shows a glandular disc in addition to the mamilliform gland. The colour pattern of *E. pulchella* is of relatively coarse tessellation of brown to black spots, aligned in oblique series on a pale ground, often appearing as a black shell with large white spots. In contrast, the shell of *A. knysnaensis* has a finely speckled brown pattern; this is visible on the base even in those that are almost black above the periphery, as is frequent in samples from Namibia.

Hughes (1979) mentioned and illustrated unusually elongated shells from Arniston (Fig. 19F). Some of these have been dissected and found to contain trematode parasites, which were presumably responsible for the distortion. Kilburn (1972) reported that the peripheral keel was more well developed in samples from wave-exposed shores, whereas it was said to be absent in estuarine shells, which were also found to be larger in size. The largest examples seen in the present study were from the Atlantic coast.

Afrolittorina praetermissa (May, 1909)

Figs. 17E,F, 22–24, 25C–E

?Litorina ziczac.—Philippi, 1847: 162–163 (not *Trochus ziczac* Gmelin, 1791 = *Echinolittorina ziczac*; in part; includes *E. ziczac*; inclusion in synonymy based on locality Kangaroo Island).

Littorina ziczac.—Tenison Woods, 1879: 69 (not Gmelin, 1791; in part; includes *E. ziczac*).

Littorina philippii.—Angas, 1865: 172 [not *Litorina philippii* Carpenter, 1857 = *Echinolittorina apicina* (Menke, 1851)]. Tenison Woods, 1878: 36 (as *philippi*; not Carpenter, 1857). Gatliff, 1887: 60 (as *phillippi*; not Carpenter, 1857).

Littorina undulata.—Angas, 1865: 172 (not Gray, 1839 = *Littoraria undulata*). Tenison Woods, 1878: 36 (not Gray, 1839).

Littorina paludinella.—Tenison Woods, 1878: 36 (not Reeve, 1857; see Hedley, 1913; Ponder & Rosewater, 1979). Gatliff, 1887: 60 (not Reeve, 1857). Pritchard & Gatliff, 1902: 92 (not Reeve, 1857).

Melarapha paludinella.—Macpherson & Gabriel, 1962: 89 (not Reeve, 1857).

Littorina caerulescens.—Tenison Woods, 1879: 65–72 (as *coerulescens*; not *Turbo caerulescens* Lamarck, 1822 = *Melarhaphe neritoides*; in part; includes *A. africana, Austrolittorina unifasciata, A. antipodum, Littoraria mauritiana, M. neritoides*).

Littorina unifasciata.—Haacke, 1885: 504–505 (not Gray, 1826; in part, includes *Austrolittorina unifasciata*).

Littorina mauritiana.—Tate & May, 1901: 389 (not *Phasianella mauritiana* Lamarck, 1822 = *Littoraria mauritiana*; in part; includes *Austrolittorina unifasciata*).

Littorina novaezealandiae "Reeve" Pritchard & Gatliff, 1902: 91 (unjustified emendation of *Littorina novaezelandiae* Reeve, 1857; not Reeve, 1857 = *Echinolittorina novaezelandiae*; in part; includes *E. novaezelandiae*).

Litorina praetermissa May, 1909: 57, pl. 6, fig. 3 (Tasmania; holotype TMAG E353/7694, fig. 22G, seen; 4 possible paratypes MCZ 23099, seen).

Melarhaphe praetermissa.—Hedley, 1913: 1913 (as *Melaraphe*). May, 1921: 47. May, 1923: 49, pl. 22, fig. 18. Cotton & Godfrey, 1938: 10. Macpherson & Chapple, 1951: 118 (as *Melaraphe*). Kershaw, 1955: 307 (as *Melaraphe*).

Littorina praetermissa.—Guiler, 1958: 139. Wilson & Gillett, 1979: 52, pl. 8, fig. 8, 8a.

Melarapha praetermissa.—McMichael, 1959: 27. Iredale & McMichael, 1962: 38. Macpherson & Gabriel, 1962: 87–88, fig. 116.

Littorina (Littoraria) praetermissa.—Rosewater, 1970: 423, 445–446, pl. 325, figs. 26, 27, pl. 343, pl. 344, fig. A (radula), B (penis), pl. 345 (distribution).

Littorina (Austrolittorina) praetermissa.—Ponder & Rosewater, 1979: 775, pl. 3, fig. 3 (penis). Ludbrook & Gowlett-Holmes, 1989: 564–565. Wilson, 1993: 146, pl. 18, fig. 4a,b.

Nodilittorina praetermissa.—Bandel & Kadolsky, 1982: 3.

Nodilittorina (?Nodilittorina) praetermissa.—Reid, 1989: 100.

Nodilittorina (Austrolittorina) praetermissa.—Reid, 2002*a*: 154.

Afrolittorina praetermissa.—Williams *et al*., 2003.

Taxonomic history. This species is common on the shores of southern Australia and Tasmania, so it is remarkable that it was not named until 1909. Before this, it was variously misidentified. The earliest apparent reference to the species is Philippi's (1847) record of *Litorina ziczac* from Kangaroo Island in South Australia, collected by Harvey; Philippi's figure 13 may be this species, but no locality was given. The use of the name *Littorina philippii* (Angas, 1865; Tenison Woods, 1878; Gatliff, 1887) is surprising, because this taxon was described from Mexico.

Several authors used the name *Littorina paludinella* for a juvenile form of this species that is a small, low-spired shell of brown colour with a pale basal band (Tenison Woods, 1878; Gatliff, 1887; Pritchard & Gatliff, 1902; Macpherson & Gabriel, 1962). However, Hedley (1913) examined the types of Reeve's species and found that they were a hydrobiid from Tasmania, as subsequently confirmed (Ponder & Rosewater, 1979; Ponder *et al*., 1993).

This species has sometimes been considered as a striped form of the sympatric *Austrolittorina unifasciata* (Tenison Woods, 1879; Haacke, 1885; Tate & May, 1901; see Taxonomic History of *A. unifasciata*).

Diagnosis. Shell moderately large, patulous to high-turbinate, periphery rounded, usually sculptured with incised spiral lines; pale, with brown tessellated or marbled pattern. Penis with rounded, slightly swollen filament; mamilliform gland and glandular disc on base. Pallial oviduct with three consecutive loops of egg groove, in albumen gland, capsule gland and in terminal portion of oviduct.

Material examined. 64 lots (45 AMS, 7 USNM, 9 BMNH, 1 ZMA, 1 MNHNP, 1 NMW), including 8 penes, 4 sperm samples, 6 pallial oviducts, 3 radulae.

Shell (Figs. 22, 25C–E). Mature shell height 8.2–19.4 mm (down to 3 mm, Nwe, 1974). Shape patulous to high-turbinate (H/B = 1.13–1.60; SH = 1.20–1.95); spire outline slightly concave; whorls well rounded, suture distinct, periphery rounded or slightly angled; moderately solid. Columella pillar straight to slightly concave; columella excavated; sometimes a slight pseudoumbilicus (frequent in juveniles); eroded parietal area absent. Sculpture of 13–16 primary spiral grooves above periphery, remaining as approximately equidistant incised lines, continuing faintly on base; periphery sometimes marked by a slightly raised rib; secondary division occasionally increases spiral lines to up to 22 above periphery on last whorl; prominence of spiral lines varies, juveniles are usually smooth and lines often become obsolete on last whorl; microscopically, surface is shiny with only faint spiral microstriae; spire usually eroded; growth lines may be strong at end of last whorl. Protoconch rarely preserved, about 0.34 mm diameter, 3 whorls. Colour whitish, cream or pale blue-grey; pale grey brown to dark brown pattern, finely tessellated or marbled, often aligned to form oblique axial stripes or zigzags, occasionally spiral lines; juveniles dark brown with white spiral band on base, pattern of additional pale bands and marbling appearing only on and after whorl 3 of teleoconch; aperture dark brown with basal white band.

Animal. Head and sides of foot black; tentacles with two broad longitudinal black stripes, fusing distally, sometimes completely fused to give black tentacles. Opercular ratio 0.46–0.52. Penis (Fig. 23A–E): filament 0.4–0.5 total length of penis, bluntly rounded, smooth, slightly swollen; sperm groove open to filament tip; single large mamilliform gland and adjacent smaller lobe of penial glandular disc borne together on lateral branch of base; penis unpigmented; penis regresses to a stub outside May–October breeding season (Nwe, 1974). Euspermatozoa 61–66 µm; paraspermatozoa (Fig. 23J,K) spherical to oval, 13–21 µm diameter, containing large spherical granules and one (or up to 6) small, rectangular or irregular rod-bodies that are hexagonal in section and do not project from cell. Pallial oviduct (Fig. 23F,G) with simple loop of albumen gland, followed by large, almost circular loop of capsule gland, opaque pink, within which central portion

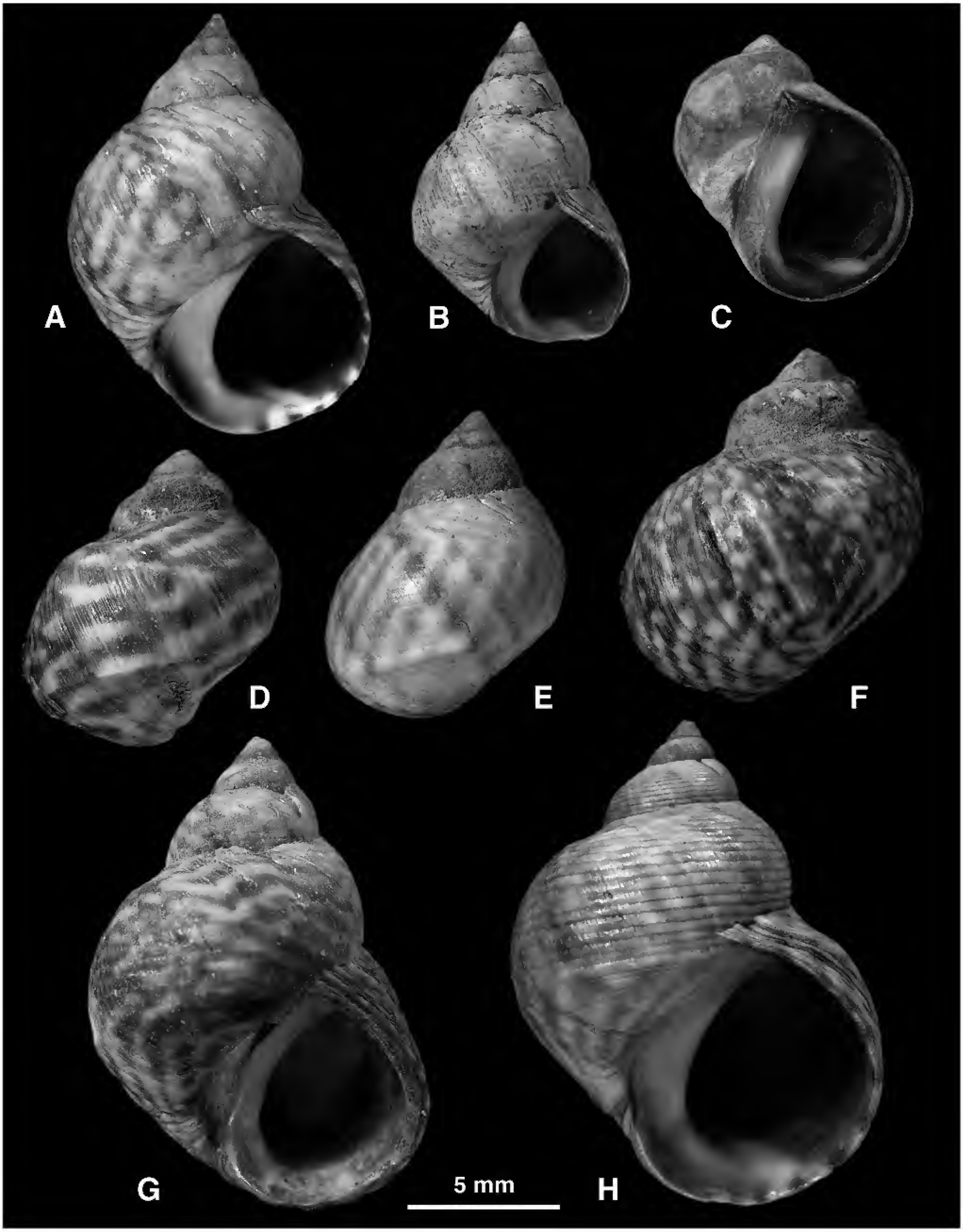

Fig. 22. *Afrolittorina praetermissa*: (*A*) southern Tasmania, Australia (BMNH 20030439). (*B*) Cape Sorrell, Tasmania, Australia (AMS C387215). (*C*) Lion Island, Recherche Archipelago, Western Australia (AMS C386849). (*D,F*) Burnie, Tasmania, Australia (AMS C387214). (*E*) Shelly Beach, Phillip Island, Victoria, Australia (BMNH 20030440). (*G*) Holotype of *Litorina praetermissa* May, 1909 (TMAG E353/7694). (*H*) London Bridge, near Port Campbell, Victoria, Australia (AMS C387216).

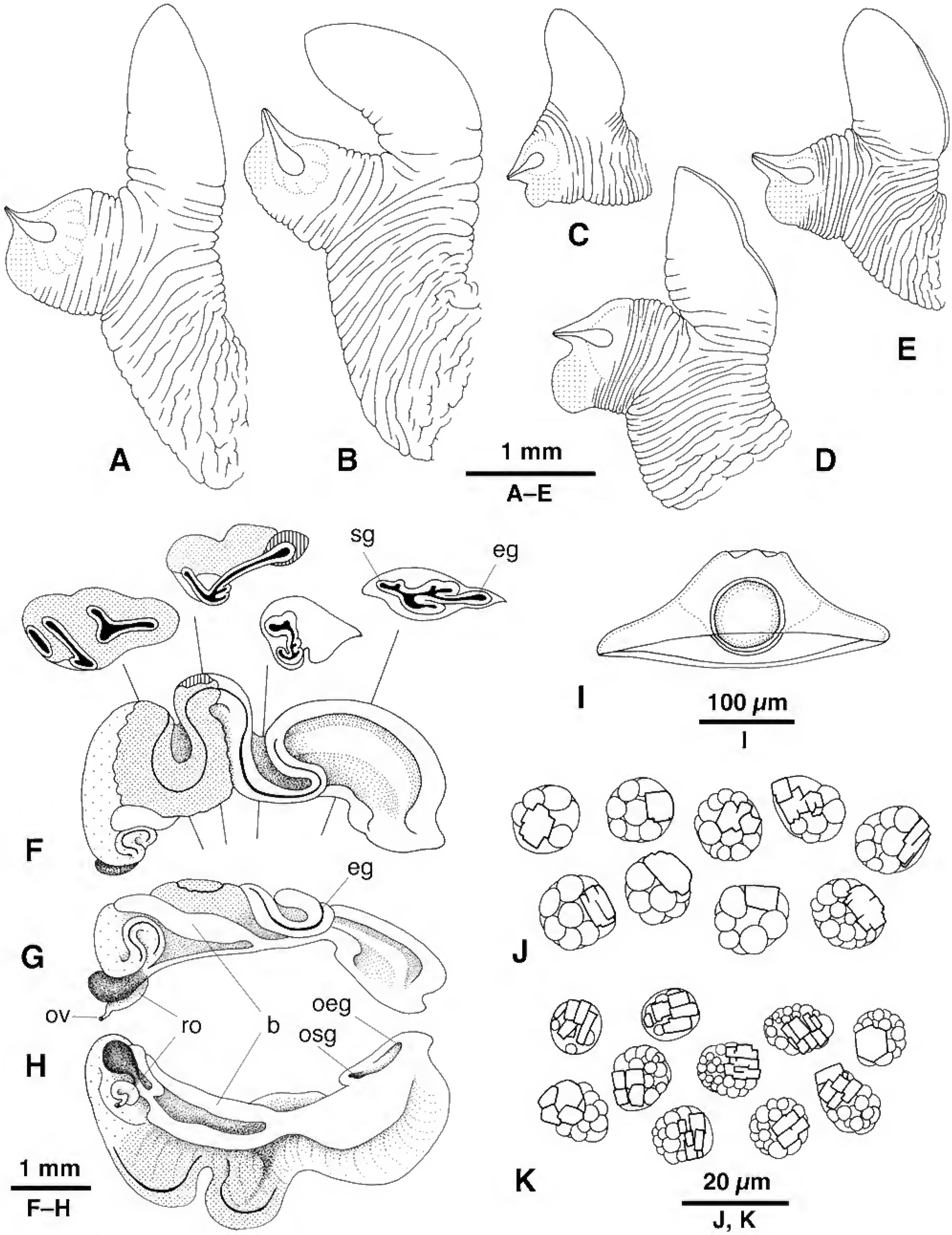

Fig. 23. *Afrolittorina praetermissa*: (*A–E*) Penes. (*F–G*) Pallial oviduct from slightly immature specimen (glands are less swollen, so that spiral route of egg groove is clearly visible; mature oviduct resembles Fig. 19H in (*F*) lateral, (*G*) ventral, and (*H*) medial views. (*I*) Egg capsule (after Nwe, 1974). (*J,K*) Paraspermatozoa from two specimens. (*A,B,F–H,J*) Pirates Bay, Eaglehawk Neck, Tasmania, Australia (BMNH 20030441). (*E,K*) Blackmans Bay, Tasmania, Australia (BMNH 20030442). (*D*) Southport, Tasmania, Australia (BMNH 20030443). (*I*) Gulf St Vincent, South Australia. Shell heights: (*A*) 9.7 mm, (*B*) 10.3 mm, (*C*) 8.5 mm, (*D*) 10.8 mm, (*E*) 8.2 mm, (*F–H*) 12.5 mm. Abbreviations: (*b*) copulatory bursa; (*eg*) egg groove (visible by transparency as line of black pigment); (*oeg*) anterior opening of egg groove; (*osg*) anterior opening of sperm groove; (*ov*) cut ovarian oviduct (from ovary); (*ro*) renal oviduct. Shading conventions as in Fig. 3.

adjacent to egg groove and distal portion are differentiated as reddish translucent capsule gland; additional simple loop of glandular material between capsule gland and terminal straight portion; copulatory bursa separates in a posterior position and continues back to overlay albumen gland.

Spawn and development. Spawn (Fig. 23I) a transparent pelagic capsule 240–300 µm diameter containing a single ovum 80 µm diameter, capsule hat-shaped with waved concentric ring on crown and wide peripheral brim; development planktotrophic; females mature July–September in vicinity of Adelaide (Nwe, 1974). Pelagic spawn also observed by F. Murray (quoted in Pilkington, 1971).

Radula (Fig. 17E,F). Relative radular length 4.1–7.6. Rachidian: length/width 1.16–1.53; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps large, elongate to rectangular, rounded to truncate at tip. Outer marginal: 7–8 cusps (12, Nwe, 1974).

Habitat. In South Australia (Womersley & Edmonds, 1958; Nwe, 1974) and Victoria (Bennett & Pope, 1953) *A. praetermissa* is less common than the abundant *Austrolittorina unifasciata*; it occupies the lower littoral fringe (overlapping with, but lower than *A. unifasciata*) and favours more sheltered habitats, where it is found on a variety of hard substrates including wooden piers, and occurs in shaded crevices. Juveniles occur lower, in the upper barnacles zone (Bennett & Pope, 1953; Ponder & Rosewater, 1979). Reports of the habitat of *A. praetermissa* in Tasmania confirm that it occurs slightly lower on the shore than *A. unifasciata* and often in more cryptic microhabitats; however, it is said to predominate at wave-exposed sites, especially on cliffs with intense spray (Guiler, 1952b,c; Bennett & Pope, 1960; Newman, 1994; contrary report by Guiler, 1955, suggests possible confusion of names of taxa). Of these two, only *A. praetermissa* occurs on the cold, strongly exposed west coast of Tasmania, where it is found over the whole rock surface (Bennett & Pope, 1960).

Range (Fig. 24). Southern Australia, from southwestern Western Australia to Tasmania and southern New South Wales. The main centre of distribution of this species is from the Eyre Peninsula (SA) along the coastline of Victoria to Wilsons Promontory, the islands of Bass Strait and the entire coastline of Tasmania. Several records are outside this range, all of which are of small numbers of juvenile or small shells. To the west, it is recorded from Point Sinclair, SA (32°06'S 133°00'E, AMS C390493, juveniles); Lion Island, Recherche Archipelago, WA (33°53'S 122°01'E, AMS C69337, 7 specimens, max. H = 8.5 mm); near Esperance, WA (33°51'S 121°53'E, AMS C390482 and C390490, 1 and 4 juveniles); Nine-Mile Beach, Esperance, WA (BMNH 20030447, 10 specimens, max. H = 4.8 mm); Hopetoun, WA (33°57'S 120°07'E, AMS C390489, 2 juveniles); south of Cowaramup, WA (33°52'S 115°05'E, AMS C390491, 1 juvenile). The species has not previously been recorded from Western Australia (unless the record of *Melarhaphe undulata* from King George Sound by Hedley, 1916, might possibly have been *A. praetermissa*). A recent record from the vicinity of Perth, WA (A. Cummings, pers. comm.; figured by Schneider, 2003: fig. 1) is based on a worn specimen of *Echinolittorina vidua* (Gould, 1859). To the east the two records from southern NSW are from Twofold Bay (37°05'S 149°54'E, AMS C356463, 2 juveniles) and Burrill Lake (35°23'S 150°27'E, AMS C427919, 1 juvenile). This confirms the occurrence in NSW recorded by Bennett & Pope (1960) and Macpherson & Gabriel (1962, as *Melarapha paludinella*), although this was denied by Ponder & Rosewater (1979).

Remarks. This species shows considerable variation in shape, from low-spired and patulous (Fig. 22C) to high-turbinate (Fig. 22B); possible correlation of this variation with habitat has not yet been investigated. Small shells are dark brown with a pale basal band (Fig. 25C–E) and do not show the typical marbled pattern of the adults; this has led to some taxonomic confusion (see Taxonomic History above). These juveniles should not be confused with any other species; at a similar size (3–4 mm) the shells of the sympatric *Austrolittorina unifasciata* are blue-grey with fine brown spiral lines (Fig. 25A,B). In southern NSW the distribution just overlaps that of *Afrolittorina acutispira*, but that small species has a more tall-spired shell (Fig. 25G–N). Adult shells of *A. praetermissa* can usually by distinguished from *Austrolittorina unifasciata* by the presence of a brown pattern of marbling, tessellation or stripes on the shell of the former; the penial filament is shorter in *A. praetermissa* and the pallial oviduct shows three consecutive loops of the egg groove, not two.

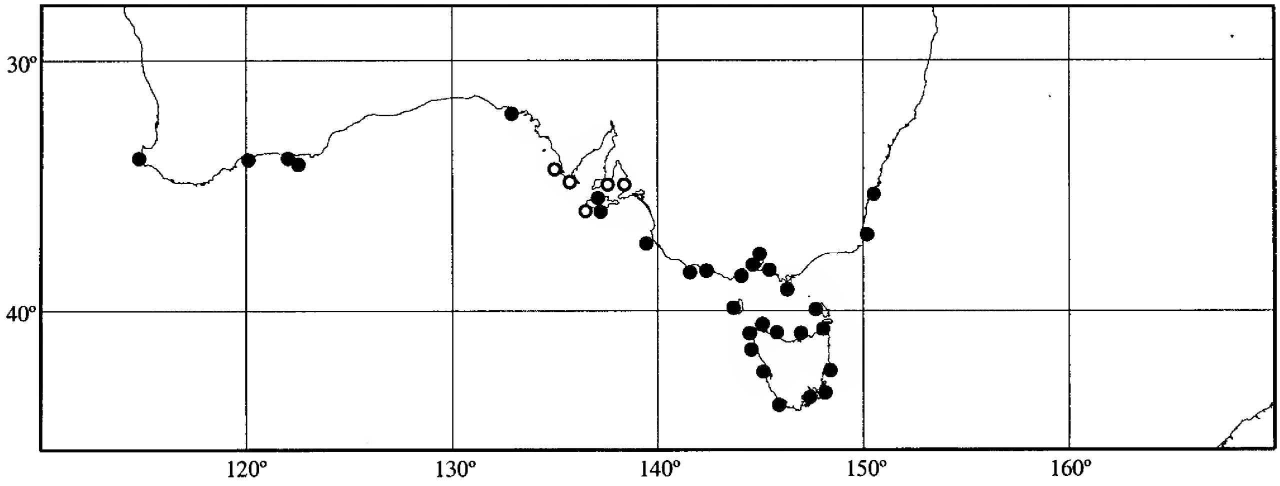

Fig. 24. Distribution of *Afrolittorina praetermissa*. Open circles are distribution records from Nwe (1974).

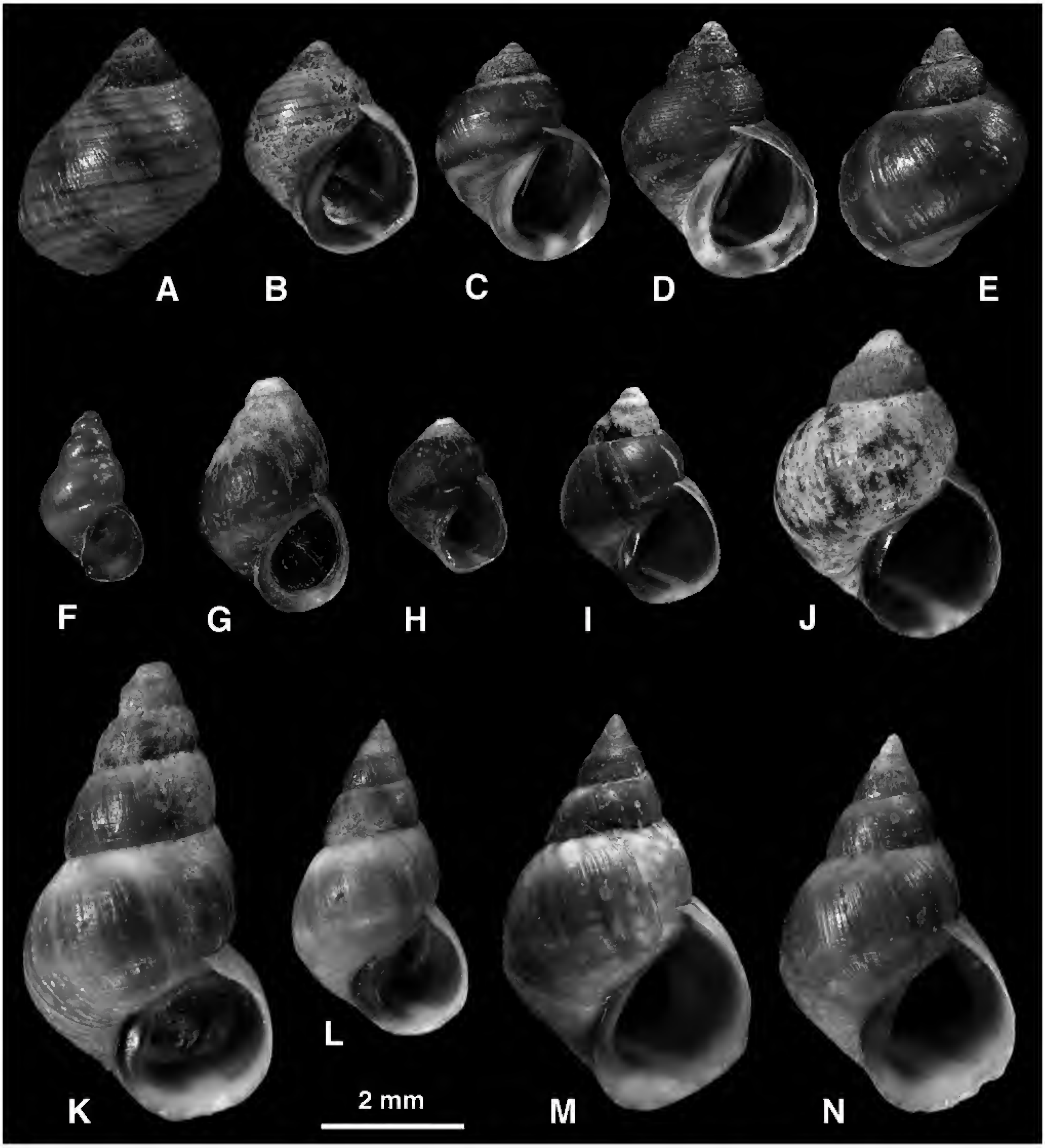

Fig. 25. Small and juvenile Australian Littorinidae. (*A,B*) *Austrolittorina unifasciata*, juvenile; Mylestom, NSW, Australia (BMNH 20030400). (*C–E*) *Afrolittorina praetermissa*, juvenile; Norman Bay, Wilsons Promontory, Victoria, Australia (AMS C387247). (*F*) *Laevilitorina mariae*; Merricks, Western Port Bay, Victoria, Australia (AMS C166157). (*G–N*) *Afrolittorina acutispira*. (*G*) Syntype of *Littorina infans* E.A. Smith, 1892; Port Jackson, NSW, Australia (BMNH 1891.11.6.226). (*H*) South side of Caloundra Gead, Queensland (AMS C387248). (*I,J*) Mrs Macquaries Point, Port Jackson, NSW, Australia (BMNH 20030444). (*K*) Green Point, Watsons Bay, Port Jackson, NSW, Australia (AMS C008909). (*L*) Lectotype of *Littorina acutispira* E.A. Smith, 1892; Port Jackson, NSW, Australia (BMNH 1891.11.6.216). (*M*) Green Point, Watsons Bay, Port Jackson, NSW, Australia (BMNH 20030445). (*N*) Green Point, Watsons Bay, Port Jackson, NSW, Australia (AMS C357030).

The present records extend the known range of this species into WA and NSW for the first time, but these outlying records are all of small or juvenile shells and might represent occasional long-distance dispersal events that do not result in permanent colonization.

This species is a characteristic member of the cool-temperate component of the southern Australian fauna (Bennett & Pope, 1953, 1960). Its predominance on wave-exposed shores in Tasmania, but preference for cryptic microhabitats on sheltered shores in Victoria and South Australia, might suggest habitat restriction in the warmer parts of its range.

Molecular data have shown that *A. praetermissa* and *A. acutispira* are sister species, with an estimated time of more than 10 million years since divergence (Williams *et al.*, 2003). Molecular estimates of age in the absence of fossil calibration are approximate, but this estimate appears to rule out divergence to the east and west of Tasmania during Pleistocene low sea-level stands when Bass Straight was dry (for examples of this common pattern see Wilson & Allen, 1987). The almost complete allopatry between this pair, despite the old divergence time, is noteworthy. As in other sister-species pairs of southern littorinines that occupy the same land masses (*Austrolittorina antipodum* and *A. cincta* in New Zealand; *Afrolittorina africana* and *A. knysnaensis* in southern Africa), the ecological and geographical separation between these two species appears to be along an axis of temperature.

Afrolittorina acutispira (E.A. Smith, 1892)

Figs. 17G,H, 25G–N, 26, 27

Littorina acutispira E.A. Smith, 1892: 487–488, pl. 40, fig. 3 (Green Point, Watson Bay, Port Jackson, New South Wales; also Parsley Bay, Port Jackson; lectotype (Rosewater, 1970: 452) BMNH 1891.11.6.216 (fig. 25L; label: "Port Jackson"), 13 paralectotypes BMNH 1891.11.6.217–225 ("Port Jackson"), 47 paralectotypes BMNH 1886.7.26.102–111 ("Parsley Bay"), all seen).

Melarhaphe acutispira.—Hedley, 1918: M51.

Melarapha acutispira.—Iredale & McMichael, 1962: 38.

Littorina (?Littoraria) acutispira.—Rosewater, 1970: 423, 451–452, pl. 349, fig. 3, pl. 350 (distribution), pl. 351, fig. 1.

Littorina (Austrolittorina) acutispira.—Ponder & Rosewater, 1979: 773–774, pl. 1, figs. 1–3. Wilson, 1993: 146, textfig.

Nodilittorina acutispira.—Bandel & Kadolsky, 1982: 3. Jansen, 1995: 31, fig. 96.

Nodilittorina (?Nodilittorina) acutispira.—Reid, 1989: 99.

Nodilittorina (Austrolittorina) acutispira.—Reid, 2002*a*: 154.

Afrolittorina acutispira.—Williams *et al.*, 2003.

Littorina infans E.A. Smith, 1892: 488, pl. 40, fig. 4 (Green Point, Watson Bay, Port Jackson [New South Wales]; 14 syntypes BMNH 1891.11.6.226–235 (Fig. 25G), seen).

Melarhaphe infans.—Hedley, 1918: M51. Dakin, 1960: 248 (as *Melaraphe*).

Melarapha infans.—Iredale & McMichael, 1962: 38.

Littorina (?Littoraria) infans.—Rosewater, 1970: 423, 452, pl. 351, fig. 2.

Taxonomic history. Smith (1892) named this species twice in the same publication, using the name *Littorina acutispira* for larger elongate shells and *L. infans* for smaller examples with eroded spires. Owing to their small size, both taxa were neglected by subsequent workers. Rosewater (1970) retained them as separate species. As first revisers, Ponder & Rosewater (1979) established the valid name.

Diagnosis. Shell small, tall-spired, smooth; pale, with brown tessellated or marbled pattern. Penis with rounded, swollen filament; mamilliform gland on narrow lateral branch of base. Pallial oviduct with three consecutive loops of egg groove, in albumen gland, capsule gland and in terminal portion of oviduct.

Material examined. 56 lots (45 AMS, 2 USNM, 9 BMNH), incl. 9 penes, 2 sperm samples, 10 pallial oviducts, 4 radulae.

Shell (Fig. 25G–N). Mature shell height 2–7.0 mm. Shape high-turbinate to tall-spired (H/B = 1.38–1.84; SH = 1.65–2.32), but may appear almost globular if spire strongly eroded; spire outline straight; whorls rounded, suture distinct; periphery rounded or slightly angled; small shells translucent, becoming solid. Columella pillar short, straight to slightly concave; columella slightly excavated; sometimes a slight pseudoumbilicus; eroded parietal area absent. Sculpture frequently microscopically smooth, but larger shells may have 11–22 spiral striae or impressed lines on last whorl, striae rarely visible on spire; surface shiny, microstriae absent; growth lines insignificant. Protoconch rarely preserved, 0.29–0.34 mm diameter, 3 whorls, terminated by sinusigera ridge, sculpture unclear. Colour: juveniles brown with spiral white band on base; larger shells cream to brown, usually with darker grey or grey-brown zone from periphery to near suture, entire surface with fine tessellation or marbling of white and pale brown, pattern not highly regular nor aligned into axial stripes, base usually paler; aperture dark brown with basal white band.

Animal. Head and sides of foot grey to black; pigmentation of tentacles varies, may be unpigmented, or with single longitudinal black line or two broad black lines. Opercular ratio 0.45–0.52. Penis (Fig. 26A–E): filament half total length of penis, swollen with subepithelial glandular tissue, bluntly rounded; sperm groove opens subterminally; single mamilliform gland (and probably also a small patch of subepithelial glandular tissue corresponding to reduced glandular disc, on ventral side of mamilliform gland, visible in histological section only) borne on narrow lateral branch of base; penis unpigmented. Euspermatozoa length unknown; paraspermatozoa (Fig. 26H,I) elongate-oval, 20–30 µm long, containing single (rarely 2) narrow rod piece, sometimes slightly projecting, cell packed with large spherical granules and one larger oval granule. Pallial oviduct (Fig. 26F,G) with simple loop of albumen gland, followed by large capsule gland forming a loop (although loop is difficult to distinguish except in juveniles where gland is less swollen); additional simple loop of glandular material between capsule gland and terminal straight portion; copulatory bursa separates in a posterior position and continues back to overlay capsule gland.

Spawn and development. Pelagic egg capsules 169–188 µm diameter (similar to those of *Austrolittorina antipodum* illustrated by Pilkington, 1971), containing single eggs 75–93 µm diameter; development planktotrophic; breeding season October/November to March/April (Underwood & McFadyen, 1983).

Radula (Fig. 17G,H). Relative radular length 1.21–1.67. Rachidian: length/width 1.12–1.47; central cusp long, sharply pointed, smaller pointed cusp on either side. Lateral: small inner cusp and three well-developed pointed cusps. Inner marginal: four well-developed pointed cusps. Outer marginal: 6–9 cusps.

Habitat. This species is one of the most abundant molluscs on the rock platforms of New South Wales (Dakin, 1960; Underwood, 1981), although often overlooked because of its small size. In a detailed study of its population dynamics Underwood & McFadyen (1983) recorded densities of up to 70000 m^{-2} at the highest levels of the littorinid zone on platforms in Botany Bay. The highest densities were found on an exposed shore, in areas where barnacles provided crevices for protection from waves. On a sheltered shore, most snails were found in shallow pools with *Enteromorpha*. In southern Queensland the species is also found among barnacles and in shallow pools (Johnston, 1917), and occupies a zone between high water of neap tides and mean sea level (Endean *et al.*, 1956), below that of the larger littorinids.

Range (Fig. 27). Southeastern Australia from New South Wales

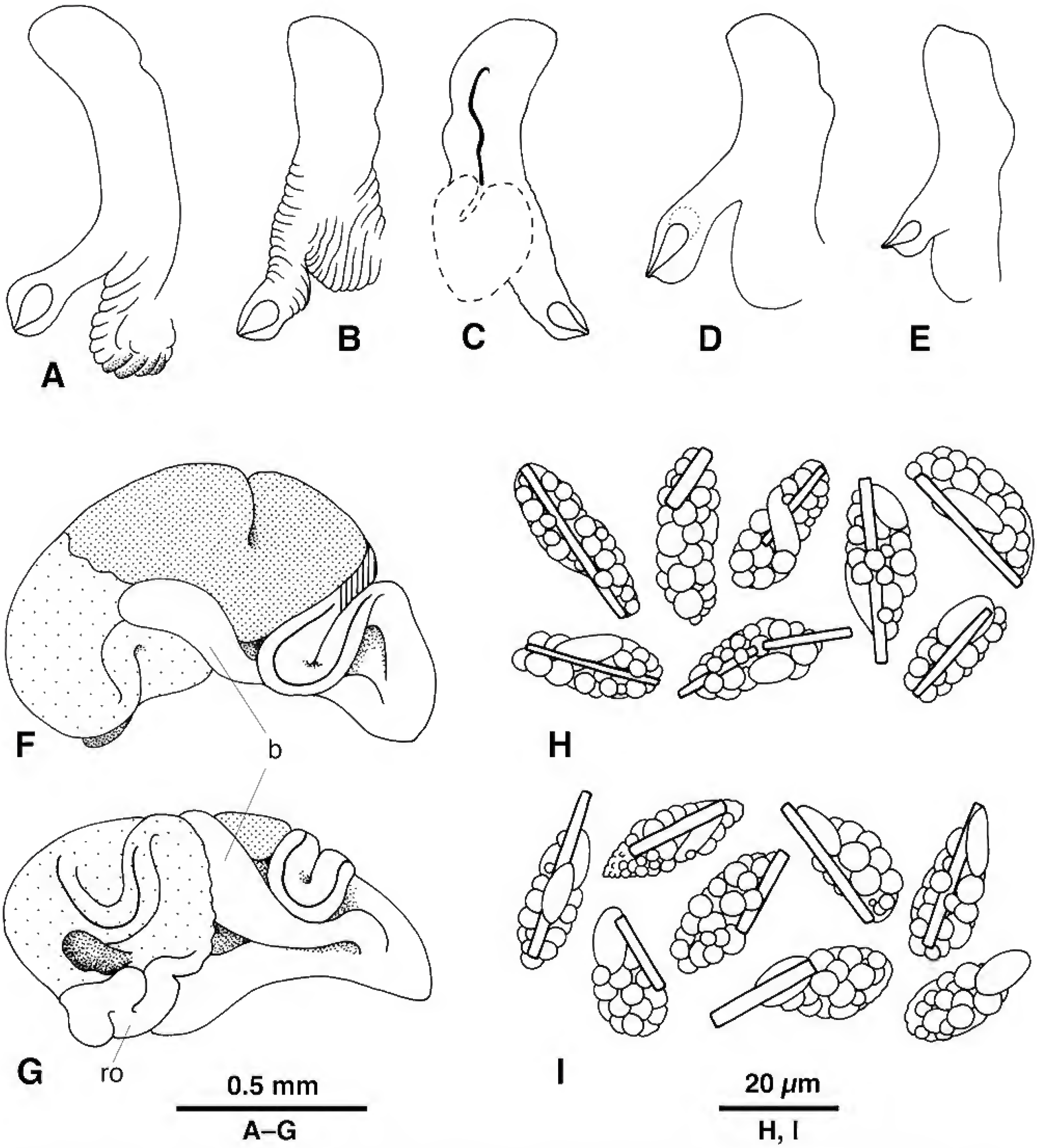

Fig. 26. *Afrolittorina acutispira*: (*A–E*) Penes (*B*) and (*C*) are lateral and medial view of same specimen). (*F,G*) Pallial oviduct of one specimen in (*F*) lateral and (*G*) ventral view. (*H,I*) Paraspermatozoa from two specimens. (*A–C,F–I*) Fairlight, North Harbour, Sydney, NSW, Australia (BMNH 20030446). (*D,E*) Bottle and Glass Rocks, Sydney Harbour, NSW, Australia (AMS C357850). Shell heights: (*A*) 3.9 mm, (*B,C*) 3.5 mm, (*D*) 3.3 mm, (*E*) 2.6 mm, (*F*) G, 4.0 mm. Abbreviations: (*b*) copulatory bursa; (*ro*) renal oviduct. Shading conventions as in Fig. 3.

to southern Queensland. This species is frequent along the entire coastline of New South Wales, the southernmost record being from Eden (37°04'S 149°54'E, AMS C357489). In Queensland it is common as far north as Noosa Heads (26°23'S 153°09'E, AMS C388093) and there are isolated records further north from Pialba, Hervey Bay (25°18'S 152°50'E, AMS C390527), Facing Island (23°49'S 151°22'E, AMS C390516), Gladstone (23°51'S 151°15'E, AMS C018502) and Yeppoon (23°9'S 150°46'E, AMS C390525). A record based on a single shell from Hayman Island (AMS C390526) requires verification.

Remarks. *Afrolittorina acutispira* is an abundant species throughout most of its range. Its small size and tall-spired, patterned shell readily distinguish it from the sympatric *Austrolittorina unifasciata*, and its habitat in pools, among algae and in barnacles is generally lower on the shore. At a similar size, juvenile shells of *Austrolittorina unifasciata* are blue-grey, with fine brown spiral lines (Fig. 25A,B). Juveniles of *Afrolittorina praetermissa* are brown with a basal pale band, like those of *A. acutispira*, but are broader (Fig. 25C–E), and that species is rare in southern New South Wales.

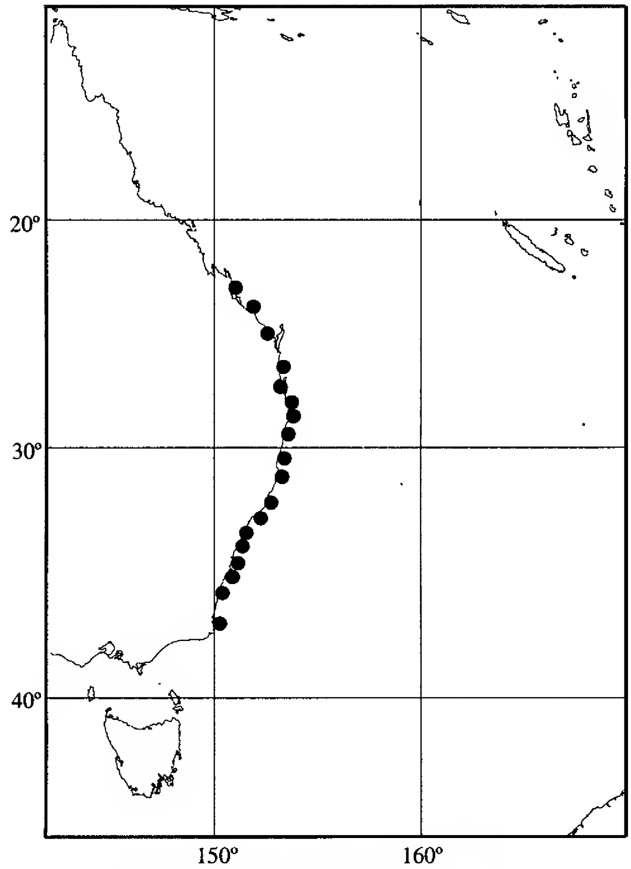

Fig. 27. Distribution of *Afrolittorina acutispira*.

In the southern parts of its range, *L. acutispira* could be confused with *Laevilitorina mariae* (Tenison Woods, 1876), which occurs among algae on littoral rock platforms, although it is uncommon in New South Wales (Ponder & Rosewater, 1979). That species is of similar elongate shape, up to 3.4 mm in height, translucent brown in colour, with a pale spiral band on the base, however the columella is narrow and not excavated and the apex is bluntly rounded, with a bulbous protoconch 0.43 mm in diameter of 1.5 whorls (indicating nonplanktotrophic development) (Fig. 25F).

The radula looks markedly different from those of other species of *Afrolittorina, Nodilittorina* and *Austrolittorina*, owing to the more equal size and sharply pointed tips of all cusps. However, these characteristics are typical of both juveniles and small species in other littorinine genera, including *Peasiella* (Reid & Mak, 1998), *Littorina* (Reid, 1996) and *Echinolittorina* (Reid, 2002*a*, as *Nodilittorina*), and are therefore interpreted as an allometric consequence of small size, perhaps connected with a different diet or feeding mechanism in small snails.

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The "Striped" Group of Stiphidiid Spiders: Two New Genera from Northeastern New South Wales, Australia (Araneae: Stiphidiidae: Amaurobioidea)

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ABSTRACT. *Borrala* and *Pillara*, two new genera of putative "stiphidiid" spiders from forest habitats in northern New South Wales, are described. They include eight new species: *Borrala dorrigo, B. webbi, B. longipalpis, B. yabbra* and *Pillara karuah, P. coolahensis, P. macleayensis, P. griswoldi*. Brief comments on characters and relationships are given. These genera form part of a generic group characterized by the presence of a palpal tegular lobe and grate-shaped tapeta in the posterior eyes.

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Borrala n.gen. and *Pillara* n.gen. are part of a distinctive group of putative stiphidiid spiders that are found in southern and eastern Australia and north to Papua New Guinea. They are characterized by the presence of a basal tegular lobe on the male palp and grate-shaped tapeta in the posterior eyes (characters they share with *Therlinya* Gray & Smith), as well as a posteriorly raised carapace. The longitudinal stripe pattern on the carapace serves as a useful field diagnostic character for the widely distributed "striped" group of genera, although it is not exclusive to them.

The genera dealt with here are known only from forest habitats of the Great Dividing Range between the Hunter River and the Border Ranges in northeastern New South Wales. The data available suggests that most of the species described here have fairly localized distributions. A second manuscript will deal with several additional "striped" group genera.

Material and methods

Specimen examinations, measurements and drawings were made using a Wild M5 or Leica M12 microscope with graticule and drawing attachment. The left male palp is illustrated. Epigynal preparations were cleared in 8% potassium hydroxide or lactic acid, before mounting in glycerol for microscopic examination. Specimen preparations for scanning electron microscopy were air dried from 100% acetone.

Abbreviations and definitions. "Tegular window" refers to the gap between the proximal embolus and the lower edge of the conductor. Carapace length for each measured specimen is followed by a range value in parentheses. BL, body length; CL, carapace length; CW carapace width; CapW, caput width; LL, labium length; LW, labium width; SL, sternum length; SW, sternum width; EGW, eye group width; AME, anterior median eyes; ALE, anterior lateral eyes; PME, posterior median eyes; PLE, posterior lateral eyes; MOQ, median ocular quadrangle; AER, anterior eye row; PER, posterior eye row; RTA, retrolateral tibial apophysis; RVTA, retrolateral ventral tibial apophysis; MA, median apophysis; Co, conductor; CyF, cymbial flange; E, embolus; TL, tegular lobe; TW, tegular window. ALS, anterior lateral spinneret; PMS, posterior median spinneret; PLS, posterior lateral spinneret; Spigots: MAP, major ampullate; mAP; minor ampullate; Cyl, cylindrical; mPLS, modified PLS; Pc, paracribellar; sAc, small aciniform; lAc, large aciniform. NP, National Park; SF, State Forest

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Repository institutions. Specimens listed under accession numbers prefixed KS are deposited in the Australian Museum, Sydney (AMS); CAS, Californian Academy of Sciences; and SAM, South Australian Museum, Adelaide.

Borrala n.gen.

Type species. *Borrala dorrigo* n.sp.

Etymology. The generic name is an Aboriginal word meaning the head of a spear, a reference to the tapering shape of the retrolateral tibial apophysis (RTA). The gender is female.

Diagnosis. Cribellate spiders. Carapace with longitudinal pigment stripes; profile highest at fovea. PME largest or subequal to AME in males. Posterior eyes with grate-shaped tapeta. Feathery hairs abundant. Cymbium with retrolateral flange, often weakly developed. Tegular lobe broad, usually basal. MA large, bipartite, with fleshy and sclerotized processes. Tibia with a large, pointed RTA, and a long, stalked ("crochet-hook") RVTA. Epigynum with a pit-like fossa, often narrowest anteriorly; spermathecae behind fossa.

Separated from *Pillara* by the presence of an undivided RTA and a bipartite MA, and from other "striped" genera by the elongate RVTA and the broad tegular lobe; separated from *Therlinya* and *Taurongia* Hogg by the striped carapace highest at fovea, and the relatively larger eyes; separated from *Stiphidion* Simon by eye rows not recurved.

Description. Medium-sized cribellate spiders (CL 1.92–3.31) which build suspended, semi-horizontal sheet webs with a shallow retreat tunnel; spiders run underneath sheet. Colour pattern (Fig. 1a; in alcohol): carapace light amber-brown, darker in front and on jaws, with narrow, grey marginal bands; eyes surrounded by black pigment, eye region dark grey with a pair of dorsolateral dark grey stripes, narrower and lighter anteriorly, darker and wider posteriorly, converging at or coalescing through the foveal region. Dorsal abdomen greyish-brown, with anterior, short, grey middorsal stripe, narrow or indistinct, set in paler lateral chevron patches continuing in decreasing size posteriorly; sides with mosaic of pale brown and grey patches, separated from grey venter by two pale, ventrolateral, longitudinal stripes; legs with distinct grey-brown bands on femora, weaker on tibiae.

Carapace with narrow, prominent caput; highest at fovea and, especially in males, rather flattened above and sloping markedly upward to fovea; foveal slit long and deep, curving down onto concave rear slope of carapace (Fig. 1c,d). Clypeus about 1.5× width of an AME. Chilum an undivided, median plate (Fig. 1e). Eyes eight, relatively large (cf.

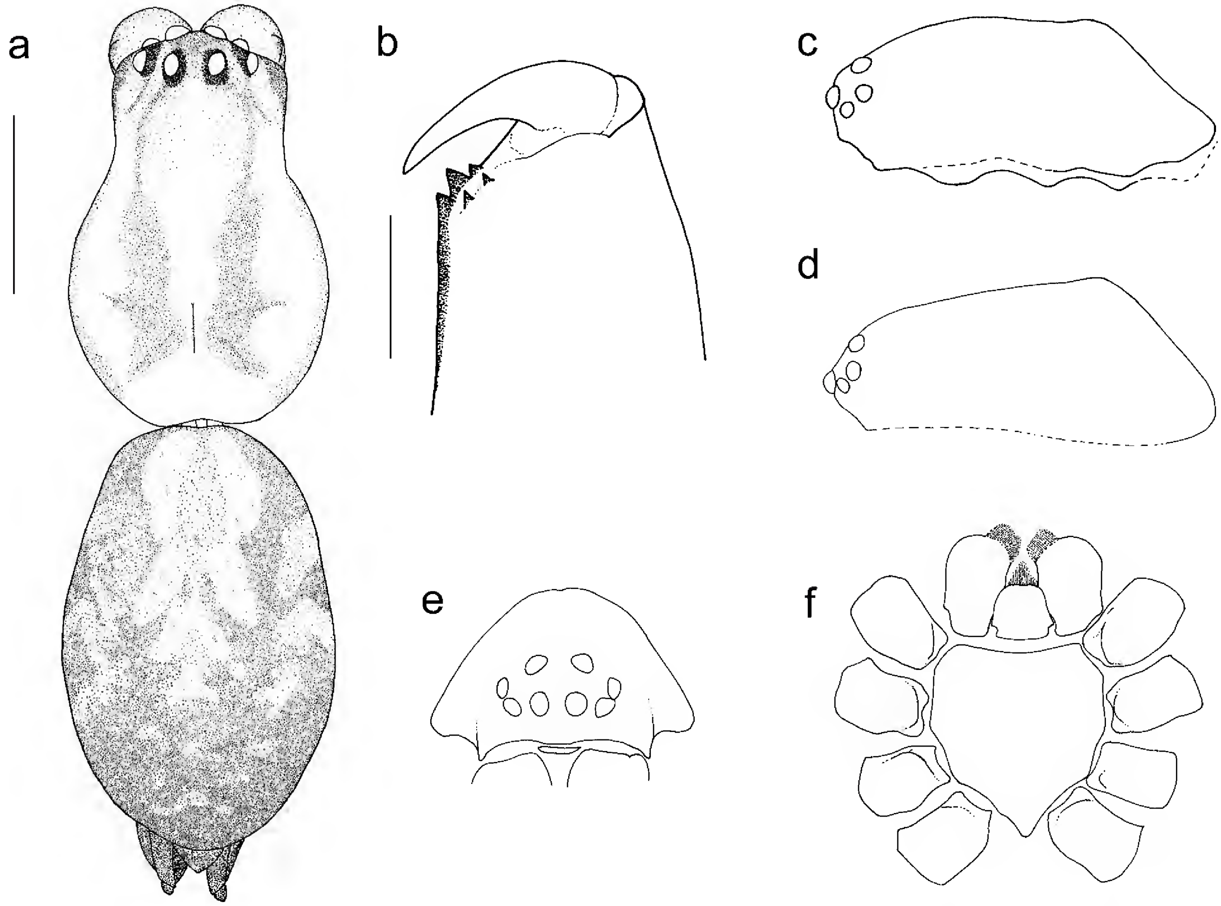

Fig. 1. *Borrala dorrigo* n.sp. (*a*) body, dorsal; (*b*) cheliceral teeth; (*c,d*) carapace, lateral: (*c*) female, (*d*) male; (*e*), carapace, frontal (eyes, chilum); (*f*), sternum, mouthparts and coxae, ventral. Scale lines: *a,c–f* 1.0 mm, *b* 0.25 mm. Specimens: *a,e–f* female KS70125, *b,c* female KS60712, *d* male KS70124.

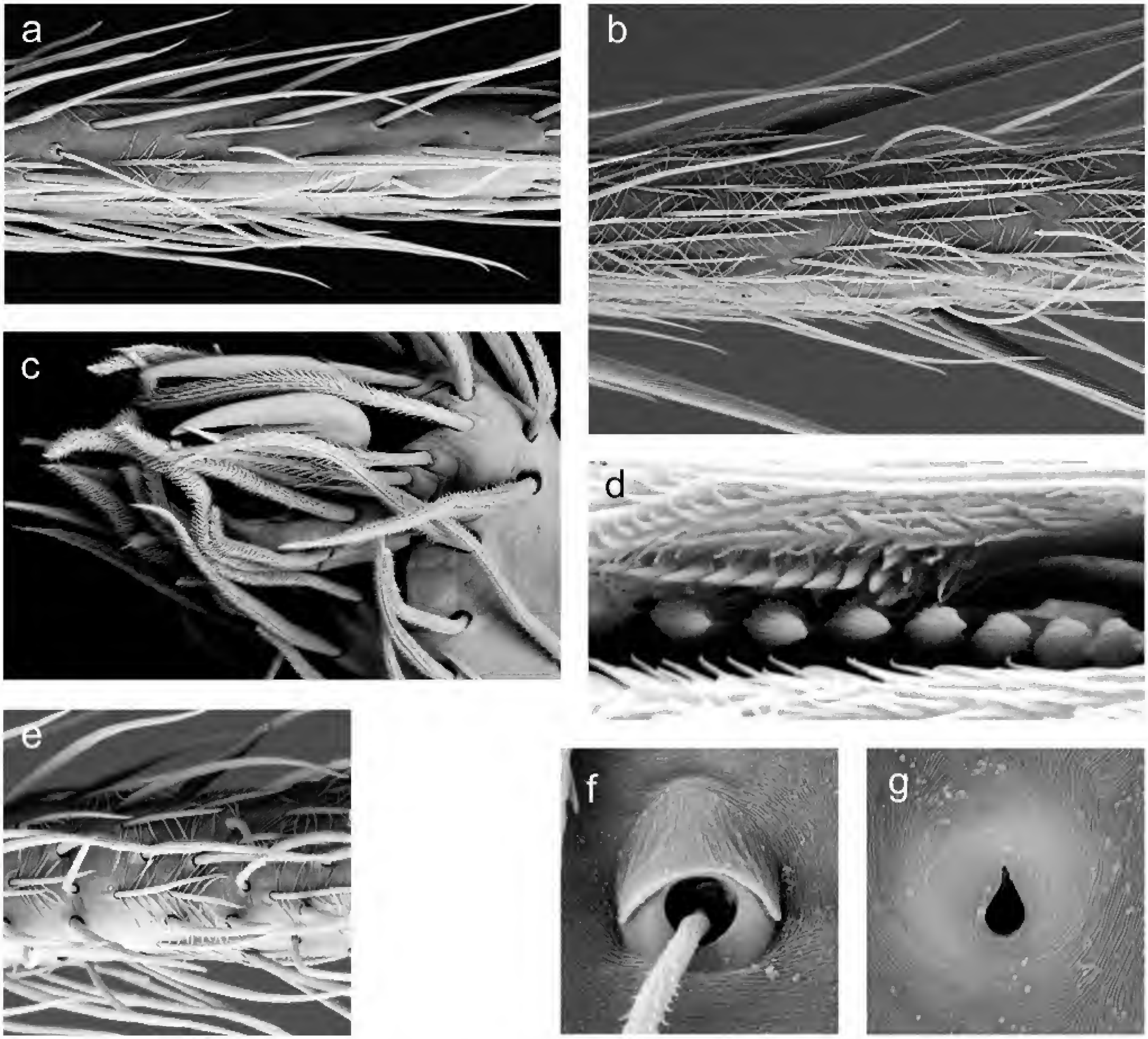

Fig. 2. *Borrala dorrigo* n.sp. (*a–g*) sensilla and claws, female KS60712, leg I: (*a*) tarsus, dorsal, hair types and tarsal organ; (*b*) metatarsus, dorsal, hair types; (*c*) tarsal claws and toothed hairs; (*d*) toothed hair and tarsal claw teeth; (*e*) tarsus, ventral, hair types; (*f*) trichobothrium base; (*g*) tarsal organ.

Therlinya), EGW three-quarters width of caput; eyes in two rows, from above AER recurved, PER procurved; eyes subequal, ALE smallest: male, AME≥PME>PLE>ALE; female, PME≥AME≥PLE>ALE. MOQ almost square, slightly narrower anteriorly (Fig. 1e). Posterior eyes with grate-shaped tapeta. Chelicerae vertical, with boss, paturon retromargin with one long, modified seta near base of each fang, numerous modified setae along promargin; fang groove with 2 retromarginal and 3 promarginal teeth, last promarginal tooth extended as a strong carina (Fig. 1b). Maxillae longer than wide, lateral margins weakly undulate to straight, strong linear serrula present. Labium length/width subequal, narrower & truncate apically, basally shortly excavated. Sternum slightly longer than wide, shortly pointed between coxa IV (Fig. 1f). Body and legs with numerous plumose and feathery hairs (Fig. 2b).

Legs slender, typically 1423 or 1243. Trochanters notched. Legs with feathery and plumose hairs, the latter either long, vertical to strongly angled distad, or shorter and curved (Fig. 2a,b,e); apical tarsus with toothed plumose hairs around claws (Fig. 2c,d). Spines: at least tibiae I & II lacking apical, paired ventral spines. Representative leg spination (*B. dorrigo*): Male (KS70124) - I: femur d122, p011; tibia d0010, v220, p101, r01010; metatarsus d2012, v221, p0101, r0101. II: femur d1202, p011; patella 001; tibia d0010, v220, p1010, r01010; metatarsus d2102, v221, p0101, r0101. III: femur d1202, p0111; patella 001; tibia d1010, v111, p0110, r0110; metatarsus d212, v221, p0101, r0101. IV: femur d1012, p001; patella 001; tibia d1010, v112, p11, r011; metatarsus d2022, v221, p0101, r0001. Female (KS70125)-I: femur d112, p011; tibia d001, v220, p1110, r1010; metatarsus d012, v221, p0101, r0101. II: femur d122, p0111; tibia d001, v220, p1110, r101; metatarsus d012, v221, p101, r101. III: femur d122, p0111; patella 001; tibia d101, v110, p0110, r0110; metatarsus d212, v221, p011, r011. IV: femur d112, p001; patella 001; tibia d101, v110, p101, r0110; metatarsus d222, v211, p0101, r001. Three tarsal claws: superior 10–11 teeth, inferior 2–3 teeth. Female palpal tarsi spinose; palpal claw with 9 teeth. Claw tufts and scopulae

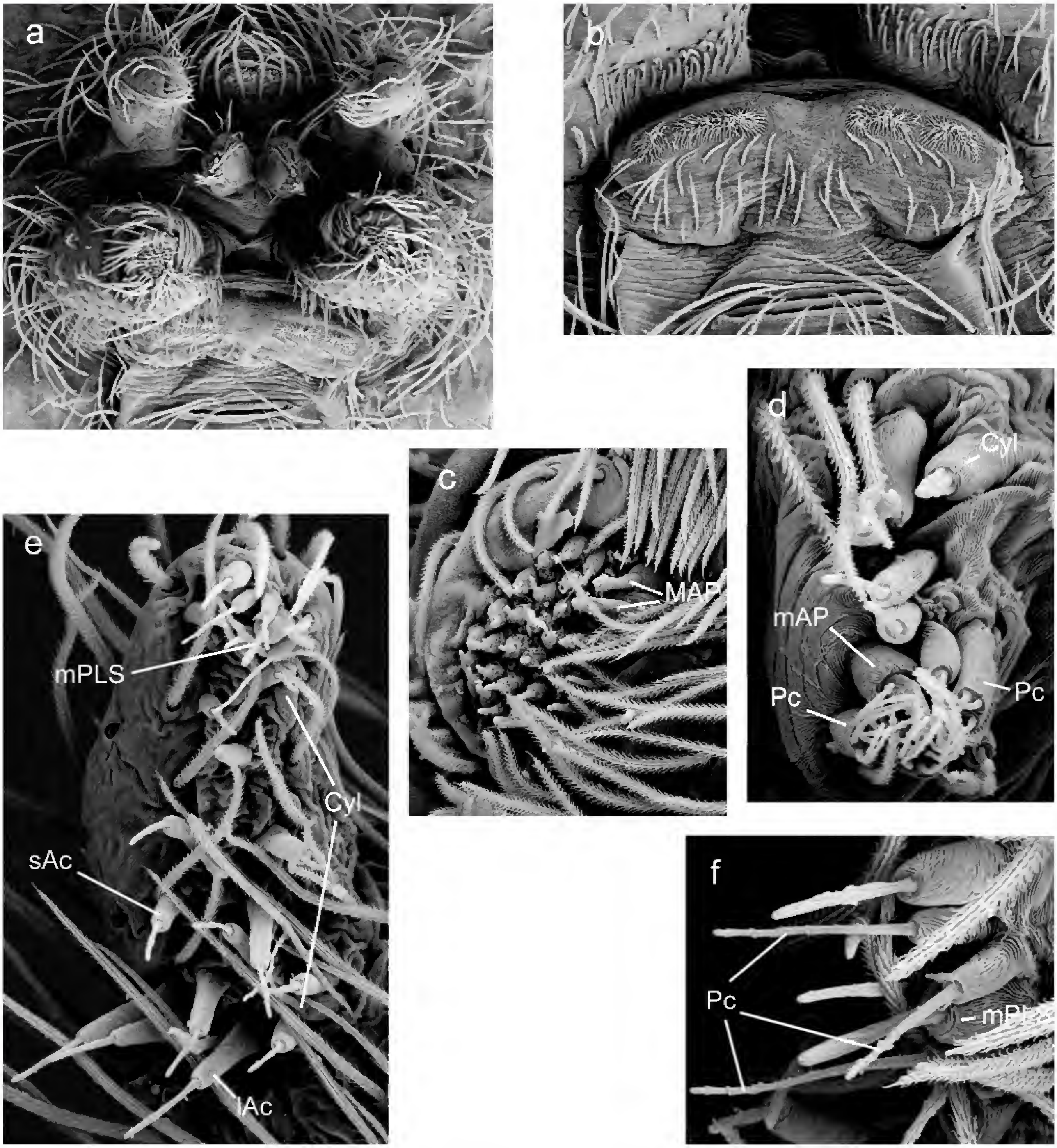

Fig. 3. *Borrala dorrigo* n.sp. (*a–f*) spinnerets, female KS60712: (*a*) spinning field (cribellum below); (*b*) cribellum and spiracle; (*c–f*) spigots: (*c*) ALS, (*d*) PMS, (*e*) PLS, (*f*) detail of PLS apex with modified PLS spigot. Spigots: *MAP* major ampullate, *mAP* minor ampullate, *Cyl* cylindrical, *mPLS* modified posterior lateral spinneret, *Pc* paracribellar, *sAc* short aciniform, *lAc* long aciniform.

absent. Trichobothria increasing in length distally, in single row on tarsi (5) and metatarsi (5–6); two rows on tibia; present on male and female palpal tarsus and tibia. Bothria collariform, proximal plate longitudinally ridged (Fig. 2f). Tarsal organ capsulate, finely longitudinally ridged, with pyriform to keyhole shaped pore (Fig. 2g), placed distal to trichobothria.

Male palp (Figs. 4a,b, 7a,b). Cymbium with a narrow flange retrolaterally and a short, coniform apex with 1–3 bristles or bristle-like spines. Tegulum with a broad tegular lobe, bluntly rounded distally and abutting the subtegulum prolaterally. Sperm duct visible as a long, rather thick, S-shaped duct looping across the basal half of the tegulum. Embolus a curved, thick, marginal rod, tapering or flattened distally, origin prolateral to basal. Conductor a thick stalk, curved retrolaterally, or weakly T-shaped, apical area with deep embolic groove and variably thickened and enlarged. Tegular window moderate-small in size, prolaterally placed. MA retrolateral to conductor base; bipartite, with a prominent, fleshy lobe ventral to a sclerotized, hooked dorsal process. Tibia longer than wide, with 2–3 long prolateral bristles and two large apophyses: RVTA arising apically, long and stalk-like with a beaked, knob-like head;

RTA arising sub-apically, large and spine-shaped. Patella usually slightly longer than wide (Fig. 7b), but longer in *B. longipalpis* (Fig. 6b).

Epigynum (Figs. 4c, 6c) moderately sclerotized, fossa an unpaired pit, either ovoid or trapezium-shaped and narrowest anteriorly. Lateral teeth and lobes absent. Internal genitalia (Fig. 4d) simple, with a pair of short, very broad copulatory ducts opening along each side of the fossa; and a pair of globose spermathecae, in contact or subadjacent medially, and placed posterior to the fossa (visible through cuticle).

Tracheal system simple, with four unbranched tracheal tubes confined to the abdomen. Spiracle just anterior to cribellum and almost half as wide as cribellum plate (Fig. 3b). Calamistrum about 0.4× length of metatarsus, subproximal-central, delimited at each end by a retrodorsal spine; weakly developed in male. Spinning organs (Fig. 3a–f, female). Cribellar plate bipartite, each spinning field over 4× as wide as long and separated by a wide seam (half of a field wide); seam and posterior plate margin strongly sclerotized, latter medially indented. In male, cribellum almost as wide as in female with small, non-functional fields. Spinnerets relatively short. ALS and PLS 2-segmented, latter slightly longer; PMS 1-segmented, shortest; ALS broad with very short apical segment with broad margins; PLS slender with moderately long, conical apical segment. Spigots (*B. dorrigo*). ALS: 2 MAP spigots, mesal, adjacent, size unequal; c. 28 piriform spigots. PMS: 3 fused paracribellar bases grouped antero-ectally, with 5–6, 8 and 6–8 spigots; 1 mAP, mesal; 6 aciniform spigots (1 anterior, rest distributed); 1 cylindrical spigot, postero-ectal. PLS: c. 18 aciniform spigots, distributed; 1 subapical "modified PLS" spigot flanked by 3 paracribellar spigots, all free; 2 cylindrical spigots (1 basal, 1 subapical).

Included species. *Borrala dorrigo, B. webbi, B. yabbra, B. longipalpis.*

Distribution. Northeastern New South Wales, Australia.

Comments. Three species, *B. longipalpis, B. dorrigo* and *B. yabbra*, show increased size and complexity of the distal conductor and flattening of the distal embolus, in contrast to the relatively unmodified conductor and embolus in *B. webbi*, the most southern species of the genus.

Several long, slender, basally placed spigots were noted on the PLS. These spigots, termed "long aciniform" here, are larger than the typical, distributed aciniform spigots (termed "short aciniform"). Such long spigots are similarly present in *Pillara, Therlinya* and *Taurongia* but they are most numerous and distributed in the *Stiphidion* PLS.

Key to *Borrala* species

Males

1 Palpal patella more than twice as long as wide .... *B. longipalpis*
—— Palpal patella only slightly longer than wide 2

2 Embolus not strongly thickened, tapering distally .... *B. webbi*
—— Embolus strongly thickened and distally flattened 3

3 Distal conductor angular and box-like, embolic groove and embolus end subapically .... *B. yabbra*
—— Distal conductor not as above, embolic groove and embolus end at conductor apex .... *B. dorrigo*

Females

1 Epigynal fossa ovoid .... *B. longipalpis*
—— Epigynal fossa more rectangular, narrowest anteriorly ("trapezium-shaped") 2

2 Lateral margins of fossa more or less straight, and of internal copulatory ducts convex .... *B. dorrigo*
—— Lateral margins of both fossa and internal copulatory ducts concave .... *B. yabbra*

Borrala dorrigo n.sp.

Figs. 1a–f, 4a–d, 8a

Etymology. The specific name is taken from the Dorrigo region, the general locality of many specimen records.

Types. **Australia, New South Wales.** HOLOTYPE ♂ KS70124, Bellinger River SF, c. 200 m along track, 30°25'S 152°45'E, 21 May 1998, H.M. Smith, as juvenile in small sheet web, matured July 1998. PARATYPES 2♀♀, 2♂♂ KS70125–8, data as holotype; ♂ KS77105, Bellinger River SF, c. 600 m along track, 30°25'03"S 152°45'30"E, 4 Feb-9 Apr 1993, M. Gray, G. Cassis, 150 m, pitfall trap, NE NSW NPWS Survey; ♂ KS57008, ♀♀ KS54029, KS57009, 3 km NE of Dorrigo, 30°19'S 152°43'E, 15 May 1998, N. Kirkwood; ♀ KS58109, Gladstone SF, Rickerbys Rd, 30°02'46"S 152°45'07"E, 25 Nov 1999, G. Milledge & H. Smith; ♀♀ KS59581, KS77106, Scotchmans Peak, west of Bellingen along Horseshoe Rd, 30°28'30"S 152°39'43"E, 11 Nov 1999, M.R. Gray, in small sheet webs in earth bank; ♀ KS59582, locality data as holotype, M.R. Gray, H.M. Smith, 12 Nov 1999; ♀ KS75358, Scotchman SF, junction of Horseshoe Rd & Little Boggy Track, 30°26'S 152°48'E, 23 Nov 2001, G. Milledge & H. Smith, Stop 3, in sheet web; ♂ KS75361, locality data as holotype, 22 Nov 2001, G. Milledge & H. Smith, Stop 1, in sheet web; ♀ KS75362, Dorrigo NP, 5.5 km NW of Thora, 30°23'S 152°45'E, 22 Nov 2001, G. Milledge & H. Smith, Stop 2, in sheet web; ♀♀ KS75363, KS77107, Oakes SF, Horseshoe Rd, 1.2 km E of Sirius Rd junction, 30°29'S 152°36'E, 23 Nov 2001, G. Milledge & H. Smith, Stop 6, in sheet webs; ♀ KS75364, Diehappy SF, Orama Rd, 2.8 km from Horseshoe Rd, 30°27'S 152°40'E, 23 Nov 2001, G. Milledge & H. Smith, Stop 8, sheet web; ♂♂ NN19553–4, ♀ NN19555 (SAM), Bruxner Park, NW of Coffs Harbour, 30°14'S 153°06'E, 25–26 May 1986, D. Hirst, at base of trees.

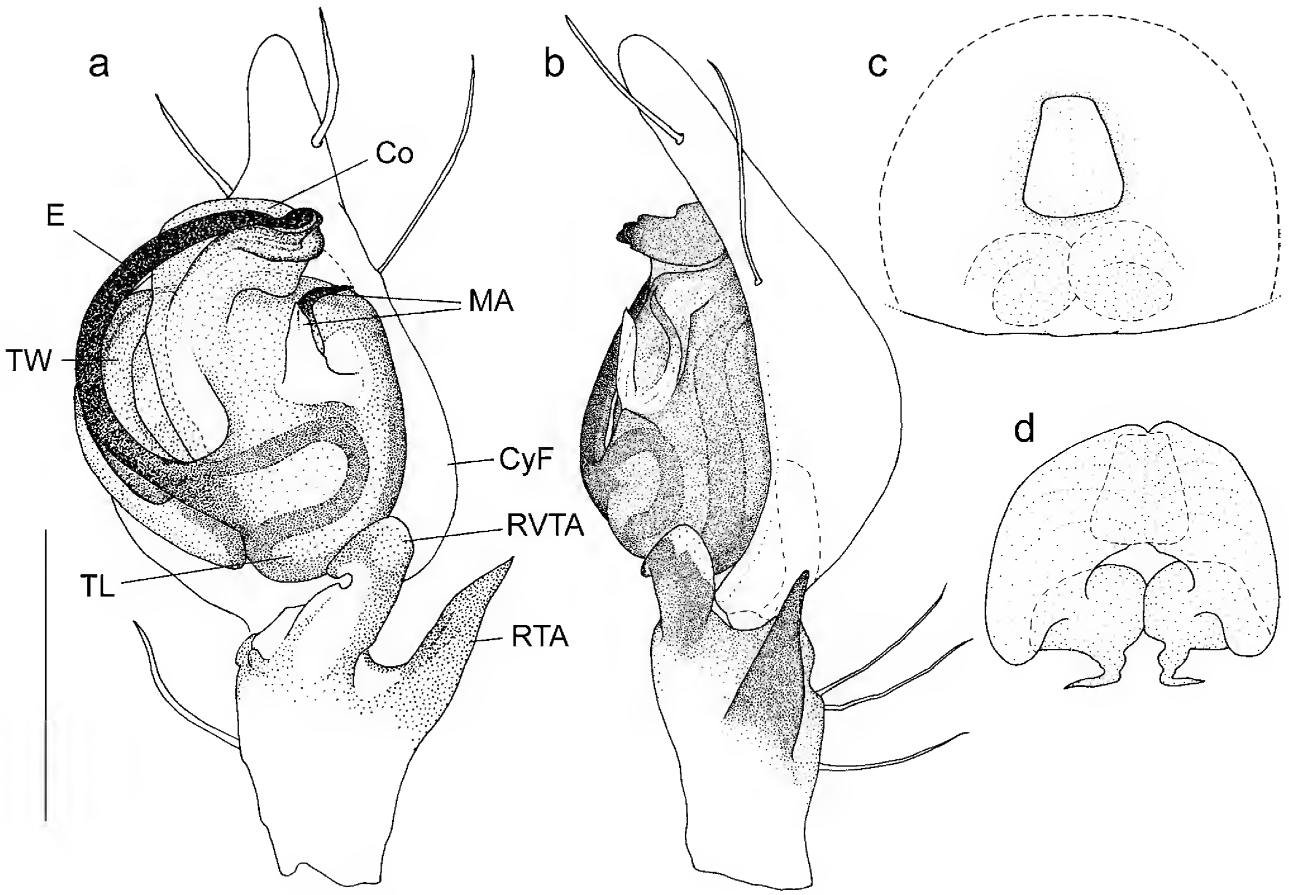

Fig. 4. *Borrala dorrigo* n.sp. (*a,b*) Male palp (KS77105): (*a*) ventral, (*b*) retrolateral. (*c–d*) Female epigynum (KS70126): (*c*) ventral, (*d*) dorsal-internal genitalia. Scale line 0.5 mm. *Co* conductor; *CyF* cymbial flange; *E* embolus; *MA* median apophysis; *TL* tegular lobe; *TW* tegular window; *RTA* retrolateral tibial apophysis; *RVTA* retrolateral ventral tibial apophysis.

Other material. **Australia, New South Wales**. ♀ KS35267, Dorrigo NP, Wonga Walk, 200 m SW of Hardwood lookout, 30°21'22"S 152°47'12"E, 4 Feb-9 Apr 1993, M. Gray, G. Cassis, 710 m, pitfall trap, NE NSW NPWS Survey; ♀ KS35760, Dome Rd, c. 2 km W of Never Never Picnic Area, about 60 m up small gully, 30°22'53"S 152°44'00"E, 4 Feb-9 Apr 1993, M. Gray, G. Cassis, 630 m, pitfall trap, NE NSW NPWS Survey; ♂ KS35768, Bellinger River SF, c. 600 m along track, 30°25'03"S 152°45'30"E, 4 Feb-9 Apr 1993, M. Gray, G. Cassis, 150 m, pitfall trap, NE NSW NPWS Survey; ♀ KS60712, locality data as holotype, M.R. Gray, H.M. Smith, 12 Nov 1999, abdomen used for SEM; ♀♀ NN19556–7 (SAM), Bruxner Park, NW of Coffs Harbour, 30°14'S 153°06'E, 25–26 May 1986, D. Hirst, at base of trees.

Diagnosis. Separated from all species except *B. yabbra* by the thick, flattened embolic tip. Embolus longer than in *B. yabbra* and embolus and conductor groove reach almost to the end of the conductor (ventral view). Epigynal fossa trapezium-shaped, lateral margins usually straight.

Male (holotype). BL 4.73, CL 2.29 (2.29–3.31), CW 1.63, CapW 0.82, EGW 0.67 LL 0.35, LW 0.35, SL 1.14, SW 1.08. Legs: 1243 (I: 12.49; II: 10.16; III: 8.33; IV: 10.08); ratio tibia I length:CW = 1:0.51. (Male palp of KS77105 illustrated in Fig. 4a,b). Patella only slightly longer than wide. RTA robust, tapers rapidly from subapical region. Conductor a thick, sclerotized stalk, distally expanded with deep, wide groove supporting distal part of embolus. Embolus a thick, strongly curved rod, flattened distally, tip extending almost to end of conductor. Tegular window of moderate size.

Female (KS70125). BL 4.98, CL 2.33 (1.92–2.65), CW 1.55, CapW 1.02, EGW 0.75, LL 0.33, LW 0.35, SL 1.10, SW 1.06. Legs: 1423 (I: 9.43; II: 7.51; III: 6.29; IV: 7.63); ratio tibia I length:CW = 1:0.64. Epigynum: (KS70126: Fig. 4c). Shallow, trapezium-shaped fossa, narrowest anteriorly; lateral margins more or less straight, rather than concave. Internal genitalia: (KS70126: Fig. 4d). Copulatory ducts broad, lateral margins strongly convex. Spermathecae in broad contact medially.

Variation. Shape of epigynal fossa sometimes less symmetrical.

Distribution. Bellinger to Nymboidea River region, eastern slopes of Great Dividing Range, mid northeastern New South Wales.

Borrala yabbra n.sp.

Figs. 5a–e, 8a

Etymology. The specific name is taken from Yabbra Scrub, Yabbra State Forest, one of the type localities.

Types. **Australia, New South Wales**. HOLOTYPE ♂ KS70129, Wiangaree State Forest, NSW, 28°23'S 153°06'E, 16 Oct 1974, M.R. Gray. PARATYPES: ♀ KS57382, Yabbra Scrub, Yabbra SF, 28°38'S 152°30'E, 14 Dec 1988, Smith, Hines, Pugh & Webber, pitfall trap Y5,

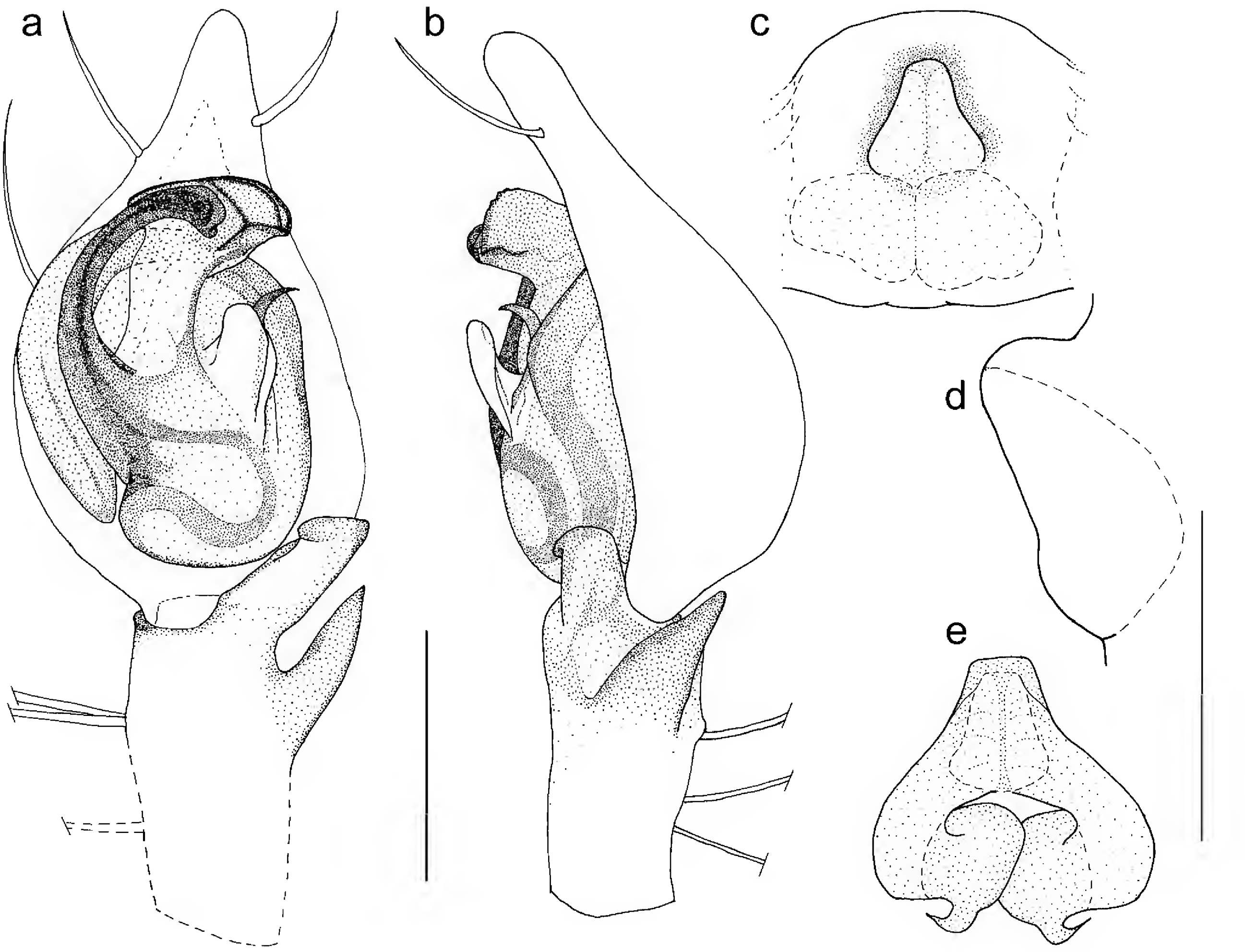

Fig. 5. *Borrala yabbra* n.sp. (*a,b*) Male palp (KS34758): (*a*) ventral, (*b*) retrolateral. (*c–e*) Female epigynum (KS57682): (*c*) ventral, (*d*) lateral, (*e*) dorsal-internal genitalia. Scale lines 0.5 mm.

dry subtropical rainforest, sheltered gully, 300–600 m, Focal Peaks Survey, UNE; ♀ KS57682, data as KS57382, pitfall trap Y2, dry subtropical rainforest, sheltered slope 600–900 m; ♂ KS34758, data as holotype; ♂ KS51321, Dome Mountain, Richmond Range & Yabbra SF, 28°28'S 152°43'E, 11 Dec 1988, Smith, Hines, Pugh & Webber, pitfall trap DM1, subtropical rainforest, swamp edge, sheltered, 600–900 m, Focal Peaks Survey, UNE.

Other material. **Australia, New South Wales**. ♂ KS57381, Yabbra Scrub, Yabbra SF, 28°38'S 152°30'E, 14 Dec 1988, Smith, Hines, Pugh & Webber, pitfall trap Y8, dry subtropical rainforest, 300–600 m, Focal Peaks Survey, UNE; ♂ KS57383, data as KS57381 but trap Y4, sheltered slope; ♂ KS60763, Dome Mountain, Richmond Range & Yabbra SF, 28°28'S 152°43'E, 11 Dec 1988, Smith, Hines, Pugh & Webber, pitfall, DM3, on unnamed peak to W of Dome Mtn, Focal Peak Survey, UNE; ♂ KS57687, data as KS60763 except trap DM6, road in subtropical rainforest, exposed ridge; ♂ KS51295, Beaury SF, Tooloom Scrub, 28°35'S 152°22'E, 12 Dec 1988, Smith, Hines, Pugh & Webber, pitfall trap T7, bunya pine plantation, sheltered ridge, 600–900 m, Focal Peaks Survey, UNE; ♀♀ & juv. KS9231, Washpool SF, Coobadjah Ck, 0.6 km from Moongem Rd, 29°16'S 152°22'E, 10 Feb 1982, C. Horseman; ♂ KS38094, Washpool SF, 29°16'S 152°22'E, 6–22 Feb 1992, M. Gray & P. Croft, Site 17C, Trap 9.

Diagnosis. Separated from all species except *B. dorrigo* by the thick, flattened embolic tip. Distal conductor more expanded and angular, and embolus shorter than in *B. dorrigo*. Epigynal fossa trapezium-shaped, lateral margins usually concave.

Male (holotype). BL 7.04, CL 3.24 (2.65–3.24), CW 2.25, CapW 1.31, EGW 0.99, LL 0.47, LW 0.47, SL 1.50, SW 1.39. Legs: 1243 (I: 18.53; II: 15.13; III: 11.85; IV: 15.00); ratio tibia I length:CW = 1:0.45. Male Palp: (Fig. 5a,b). Patella only slightly longer than wide. RTA robust, tapering from broad base. Conductor a thick, sclerotized stalk, strongly expanded distally (angular, box-like) and extending retrolaterally and ventrally beyond the end of the wide embolic groove and embolus apex. Embolus a relatively short, thick, curved rod, distal part flattened and curving ventrally in the embolic groove. Tegular window smaller than in *B. dorrigo*.

Female (KS57382). BL 5.76, CL 2.73 (2.20–2.73), CW 1.88, CapW 1.27, EGW 0.92, LL 0.41, LW 0.41, SL 1.33, SW 1.14. Legs: 1423 (I: 10.86; II: 8.78; III: 7.47; IV: 9.18); ratio tibia I length:CW = 1:0.69. Epigynum: (KS57682; Fig. 5c,d). Shallow, trapezium-shaped fossa, narrowest anteriorly; lateral margins usually weakly concave, rather than straight. Internal genitalia: (KS57682; Fig. 5e). Copulatory ducts broad, lateral margins weakly concave proximally, then convex. Spermathecae in broad contact medially.

Distribution. Clarence River catchment from the northern Richmond Range to the Washpool State Forest region, NE New South Wales.

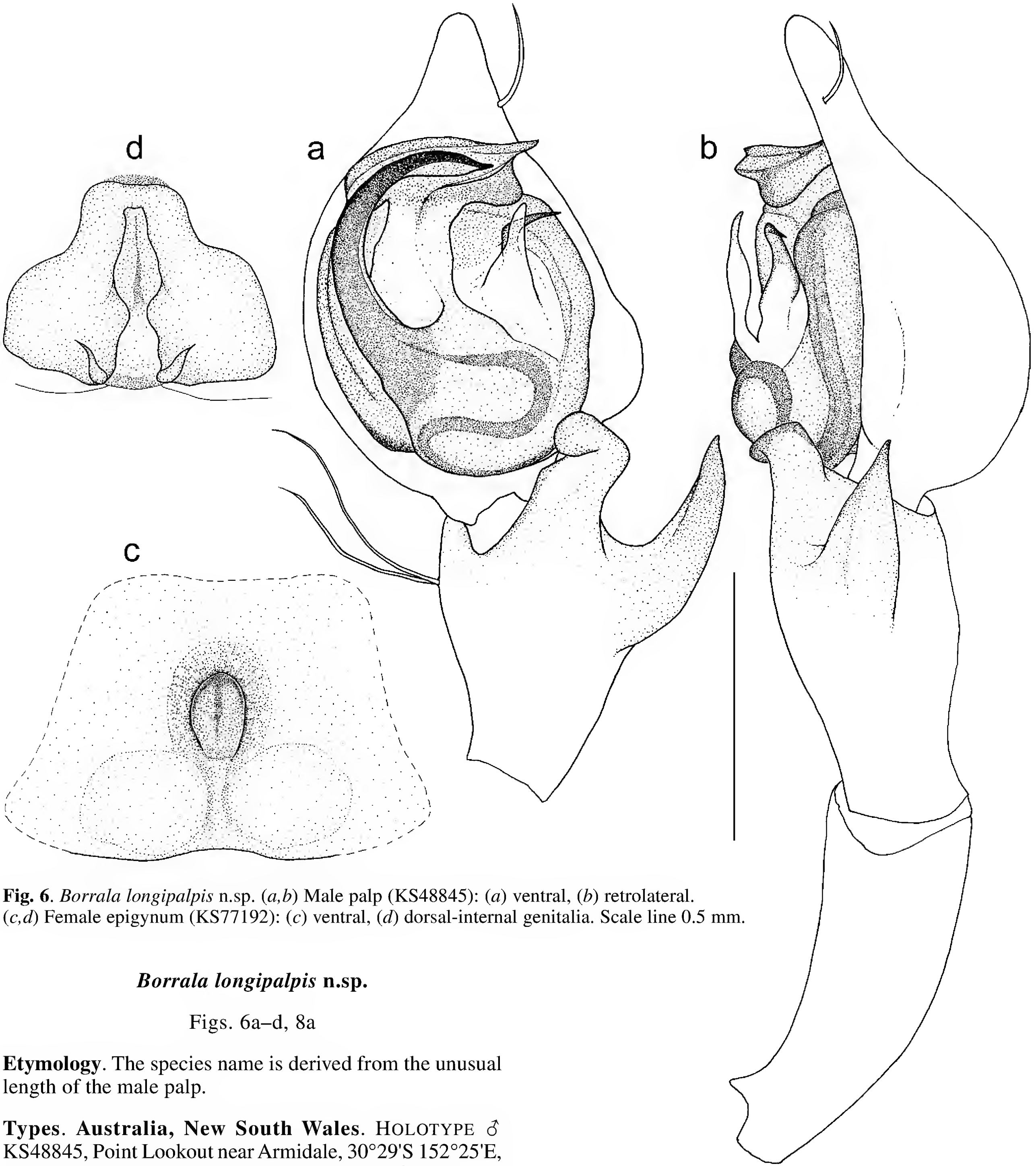

Fig. 6. *Borrala longipalpis* n.sp. (*a,b*) Male palp (KS48845): (*a*) ventral, (*b*) retrolateral. (*c,d*) Female epigynum (KS77192): (*c*) ventral, (*d*) dorsal-internal genitalia. Scale line 0.5 mm.

Borrala longipalpis n.sp.

Figs. 6a–d, 8a

Etymology. The species name is derived from the unusual length of the male palp.

Types. **Australia, New South Wales**. HOLOTYPE ♂ KS48845, Point Lookout near Armidale, 30°29'S 152°25'E, Nov 1969, M.R. Gray, damp forest. PARATYPE ♀ KS77192, data as holotype.

Diagnosis. Male palpal patella clearly longer than in other species (Fig. 6b [cf. Fig. 7b]). Epigynal fossa ovoid.

Male (holotype). BL 5.02, CL 2.45, CW 1.84, CapW 1.02, EGW 0.75, LL 0.35, LW 0.35, SL 1.16, SW 1.14. Legs: 1423 (I: 10.94; II: 9.18; III: 7.92; IV: 9.47); ratio tibia I length:CW = 1:0.69. Legs somewhat shorter than in other species. Male Palp: (Fig. 6a,b). Femur and patella relatively elongate, patella about 2.5× longer than wide; tibia robust. RTA large and very thick basally. Cymbium apical area relatively shorter and with fewer bristles (0–1); cymbial flange of moderate size. Conductor T-shaped; "head of T" short and wide, the retrolateral end shallowly bifurcate with the broad embolic groove ending upon the upper, sclerotized, beak-like process. Embolus thick basally, gradually tapering until flattening distally into a wide, translucent flange with a thicker dorsal edge and pointed apex. Tegular window small.

Female (KS77192). BL 6.04, CL 2.37, CW 1.67, CapW 1.10, EGW 0.73, LL 0.33, LW 0.37, SL 1.12, SW 1.06. Legs: 1423 (I: 8.49; II: 7.02; III: 6.04; IV: 7.31); ratio tibia I length:CW = 1:0.82. Legs somewhat shorter than in other species. Epigynum: (KS77192; Fig. 6c). Strongly

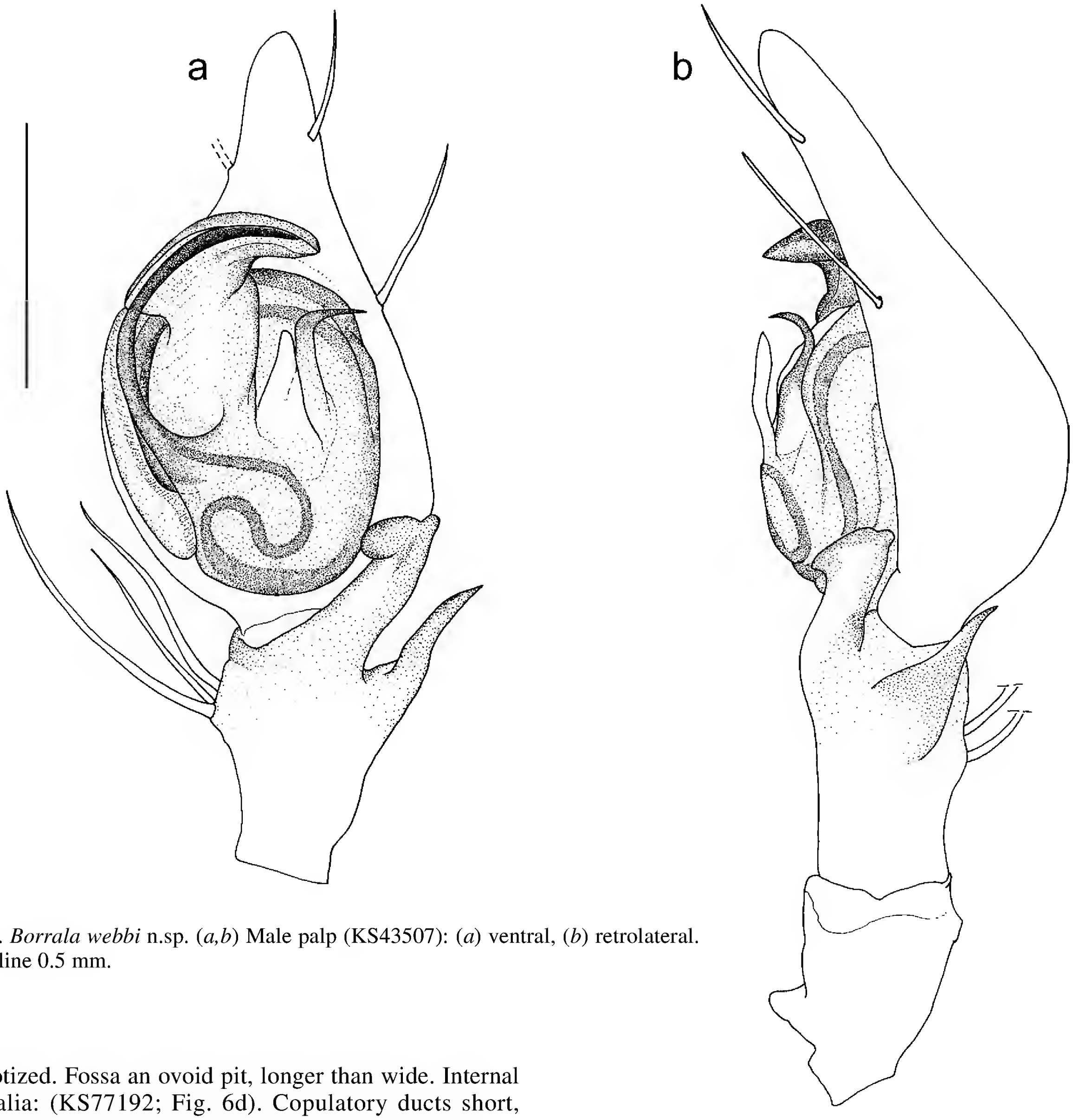

Fig. 7. *Borrala webbi* n.sp. (*a,b*) Male palp (KS43507): (*a*) ventral, (*b*) retrolateral. Scale line 0.5 mm.

sclerotized. Fossa an ovoid pit, longer than wide. Internal genitalia: (KS77192; Fig. 6d). Copulatory ducts short, straight and relatively narrow. Spermathecae adjacent, slightly separated medially.

Distribution. Known only from the type locality on the edge of the New England escarpment.

Borrala webbi n.sp.

Figs. 7a,b, 8a

Etymology. The species is named for of the collector of the types, G.A. Webb.

Types. **Australia, New South Wales**. HOLOTYPE ♂ KS43507, Mt Boss SF (Fenwicks), 31°12'S 152°24'E, Oct 1980, G.A. Webb, Forestry Commission. PARATYPES ♂♂ KS72861 & KS72862, data as holotype; ♂ KS44143, Werrikimbe NP, North Plateau, 31°15'S 152°14'E, 28 Dec 1993, D. Bickel, beech forest.

Other material. **Australia: New South Wales**. ♂ KS17667, Mt Boss SF (Thumb), 31°12'S 152°24'E, Oct 1980, G.A. Webb, Forestry Commission.

Diagnosis. Distinguished from all other members of the genus by the simple, beak-like distal conductor.

Male (holotype). BL 6.33, CL 3.10 (2.37–3.10), CW 2.29, CapW 1.31, EGW 0.86, LL 0.49, LW 0.47, SL 1.49, SW 1.33. Legs: 423 (I: not available; II: 13.42; III: 11.42; IV: 13.50). Male Palp: (Fig. 7a,b). Patella only slightly longer than wide. RTA tapering rapidly from broad base to spine-like apex. RVTA with a retroapical tubercle. Sperm duct relatively thinner and more sinuously S-looped on tegulum. Conductor weakly T-shaped, beak-like distally, with a deep embolic groove along apical margin. Embolus relatively narrow basally and of only moderate thickness, not flattened distally. Tegular window small.

Female. Not known.

Distribution. Northern Hastings River catchment, eastern Great Dividing Range, mid-northeastern New South Wales.

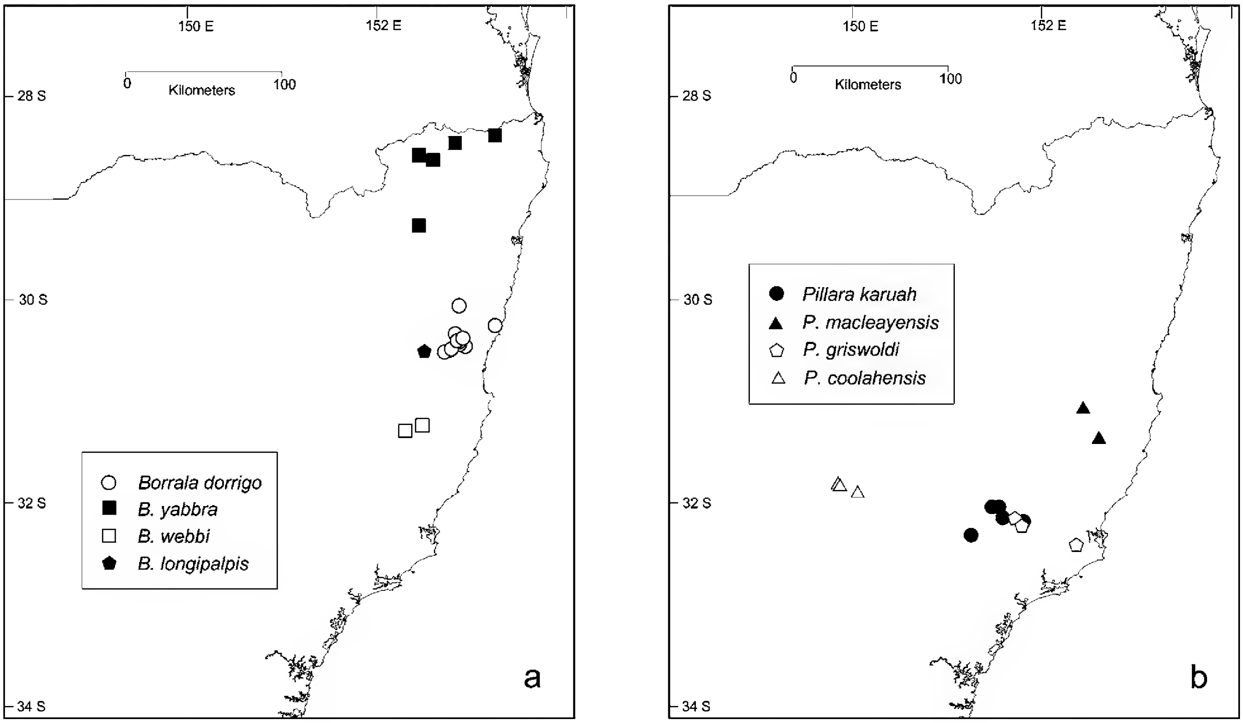

Fig. 8. Locality records for *Borrala* n.gen. (map *a*) and *Pillara* n.gen. (map *b*) species, northeastern New South Wales.

Pillara n.gen.

Type species. *Pillara karuah* n.sp.

Etymology. The generic name is an aboriginal word for a two-barbed spear, a reference to the deeply bifurcate retrolateral tibial apophysis (RTA) in this genus. The gender is female.

Diagnosis. Cribellate. Carapace with longitudinal stripes, highest at fovea. AME or PME largest. Posterior eyes with grate-shaped tapeta. Feathery hairs abundant. Cymbium retrolateral flange usually weakly developed (except *P. coolahensis*). Tegular lobe broad, basal or retrolateral. MA a weakly sclerotized or membraneous hook or reduced. Tibia with a large, bifurcate RTA, and an elongate "crochet-hook" shaped RVTA. Epigynum with a deep, unpaired fossa, round to ovoid in shape (except in *P. griswoldi*); spermathecae behind fossa.

Separated from *Borrala* and other "striped" genera by the presence of the deeply bifurcate RTA; and from *Therlinya* and *Taurongia* by this and presence of striped carapace, highest at fovea.

Description. Medium-sized cribellate spiders (CL 2.04–3.67). Similar to *Borrala* n.gen. (Figs. 1a–f, 2a–g). Eyes: male, AME> PME> PLE> ALE; female, PME> AME≥ ALE> ALE. Representative leg spination (*P. karuah*): Male (KS34509)-I: femur d122, p011; tibia d0010, v220, p1010, r1010; metatarsus d20102, v20201, p0101, r0101. II: femur d1203, p0110; patella 01; tibia d0010, v220, p1010, r01010; metatarsus d2102, v2021, p0101, r0101. III: femur d1202, p0111; patella 01; tibia d1010, v112, p0110, r0110; metatarsus d2102, v2021, p0101, r0101. IV: femur d1102, p0001; tibia d1010, v111-2, p1010, r1010; metatarsus d2022, v2021, p0101, r0001. Female (KS58361)-I: femur d122, p011; tibia d0010, v0220, p1110, r1010; metatarsus d0102, v2021, p0101, r0101. II: femur d1202, p0011; tibia d010, v0120, p110, r110; metatarsus d212, v2021, p0101, r0101. III: femur d122, p001; patella (11); tibia d110, v010, p0110, r0110; metatarsus d212, v2021, p011, r011. IV: femur d112, p001; patella (11); tibia d1010, v0110, p0101, r0110; metatarsus d222, v1021, p011, r001.

Male palp (Figs. 10a,b, 12a,b). Cymbium with a weakly to moderately developed retrolateral cymbial flange and a short, coniform-digitiform apex with 2–3 bristles. Tegulum with a broad, prominent tegular lobe, narrower than in *Borrala* and separated prolaterally from the adjacent subtegulum; lobe basally or retrolaterally placed, and usually rounded distally; lobe partially enclosing the lower part of the sinuous sperm duct. Sperm duct visible on tegulum, S-shaped, thinner and longer than in *Borrala*, its distal loop extending almost full width across ventral tegulum. Embolus a slender, marginal, curved and tapering rod, origin probasal or retrolateral. Conductor a thick sclerotized stalk, spine-like or divided retroapically; or T-shaped. Tegular window small to large, prolaterally to basally placed. MA arising retrolateral to conductor base; unipartite (see under Variation), a weakly sclerotized or membraneous hook, or reduced. Tibia short, slightly longer than or as wide, with 2–3 large, prolateral bristles; with two large apophyses: RVTA arising apically, long and stalk-like with a beaked, knob-like head; RTA arising subapically to centrally, deeply bifurcate with two large, oten digitiform, processes. Patella slightly longer than wide.

Epigynum (Figs. 10c,d, 12c,d). Moderately sclerotized, often most strongly in front of fossa (this area produced as a sclerotized knob in *P. griswoldi*); fossa an unpaired, circular to ovoid pit (except *P. griswoldi*). Lateral teeth and lobes absent. Internal genitalia (Figs. 10e, 12e) simple, with a pair of short, more or less broad copulatory ducts, curving back to a pair of roughly ovoid-circular and medially adjacent spermathecae, placed posterior to fossa (visible through cuticle).

Tracheal system simple, with four unbranched tracheal tubes confined to the abdomen. Spiracle just anterior to cribellum & less than one-third width of cribellum plate (Fig. 9b) Calamistrum about 0.4× length of metatarsus, subproximal-central, delimited at each end by a retrodorsal spine; weakly developed in male. Spinning organs (Fig. 9a–f, female). Cribellar plate bipartite, each spinning field 5–6× as wide as long and well separated by a wide seam (about 0.4× of a field wide); seam and posterior plate margin strongly sclerotized. In male, cribellum almost as wide as in female with small, non-functional fields. Spinnerets relatively short. ALS and PLS 2-segmented, latter slightly longer; PMS 1-segmented, shortest; ALS broad with very short apical segment with broad margins; PLS slender with moderately long, conical apical segment. ALS: 2 adjacent MAP spigots mesally, size unequal; c. 38 piriform spigots. PMS: 3 fully or partially fused paracribellar bases grouped antero-ectally, with 8–9, 12–13 and 6–8 spigots; 1 mAP spigot, mesal; 7–8 aciniform spigots (1 anterior, rest distributed); 1 cylindrical spigot, postero-ectal. PLS: c. 23 aciniform spigots (including group of 4–5 longest basally); 1 subapical "modified PLS" spigot flanked by 3 paracribellar spigots, all free; 2 cylindrical spigots (1 basal, 1 subapical).

Included species. *Pillara karuah, P. coolahensis, P. macleayensis, P. griswoldi.*

Variation. The MA in *P. karuah* is reduced to a membraneous spine(s) but is accompanied by a low, collar-like ridge around the spine base. This may be homologous with the fleshy process seen in the bipartite *Borrala* MA. Genitalic structure is highly derived in *P. griswoldi* (RVTA, conductor and epigynum).

Distribution. Barrington massif north to the Carrai Plateau, mid-eastern New South Wales, Australia.

Key to *Pillara* species

Males

1 Tegular lobe and embolic origin retrolaterally placed .... *P. coolahensis*

—— Tegular lobe and embolic origin probasal 2

2 Conductor divided apically; long retrolateral prong on RVTA .... *P. griswoldi*

—— Not as above 3

3 RTA bifurcation wide, processes not digitiform; MA moderately large .... *P. macleayensis*

—— RTA bifurcation narrow, processes digitiform; MA reduced .... *P. karuah*

Females

1 Epigynum with a large, sclerotized knob anteriorly, fossa absent .... *P. griswoldi*

—— Epigynum lacking knob, fossa present 2

2 Fossa small with relatively narrow copulatory ducts .... *P. macleayensis*

—— Fossa larger with wider copulatory ducts 3

3 Fossa widest anteriorly, copulatory ducts arise at front of fossa .... *P. karuah*

—— Fossa circular, copulatory ducts arise from anterolateral fossa .... *P. coolahensis*

Pillara karuah n.sp.

Figs. 8b, 10a–e

Etymology. The species name is taken from one of the major rivers arising in the distribution area of the species.

Types. **Australia, New South Wales**. HOLOTYPE ♂ KS34509, Upper Allyn, 32°10'S 151°30'E, M.R. Gray. PARATYPES ♀ KS70335, Tuglo, 48 km N Singleton, 32°14'S 151°16'E, 19 Jan 1977, M.R. Gray, sheet webs in logs extended 10–15 cm from log, rainforest; ♂ KS70332, ♀ KS70333, data as holotype; ♂♂ KS34505 & KS70336, ♀♀ KS70337–9, data as described ♀ KS70335; ♂ KS23663, Gloucester Tops, 32°04'S 151°34'E, alt. 1280 m, 19 Nov–4 Dec 1988, D. Bickel, malaise trap, nothofagus forest; ♀ KS58361, data as KS23663, 4–30 Dec 1988; ♂ KS34506, Barrington Tops, 31°58'S 151°28'E, alt. 1666 m, 18 Jul 1971, G.S. Hunt, eucalypt forest.

Other material. **Australia, New South Wales**. ♀ KS70334, data as holotype, abdomen used for SEM; ♂ KS41327, Chichester SF, 100 m N of trig tower, Berrico Rd, 32°06'S 151°45'E, 4 Feb–9 Apr 1993, M. Gray & G. Cassis, NE NSW NPWS Survey.

Diagnosis. Differs from all species except *P. macleayensis* by presence of undivided, spine-like distal conductor; from *P. macleayensis* by the reduced MA and narrowly divergent processes of bifurcate RTA. Epigynal fossa and sclerotized area in front of it larger than in *P. macleayensis*.

Male (holotype). BL 6.61, CL 3.06 (2.41–3.59), CW 2.08, CapW 1.27, EGW 0.90, LL 0.49, LW 0.49, SL 1.51, SW 1.35. Legs: 1243 (I: 17.83; II: 14.17; III: 11.83; IV: 14.00); ratio tibia I length:CW = 1:0.46. Male Palp: (Fig. 10a,b). Bifurcate RTA with two large, digitiform processes, diverging at an angle of less than 45° or subparallel, ends rounded with tip upturned and pointed. RVTA with a low retroapical ridge. Tegular lobe basal. Embolic origin probasal. Conductor stalked, bent and extended retrolaterally as a sickle-like, grooved spine. MA reduced to a short, membraneous spine (or 2 smaller spines) with a fleshy, collar-like ridge at base; or MA indistinct.

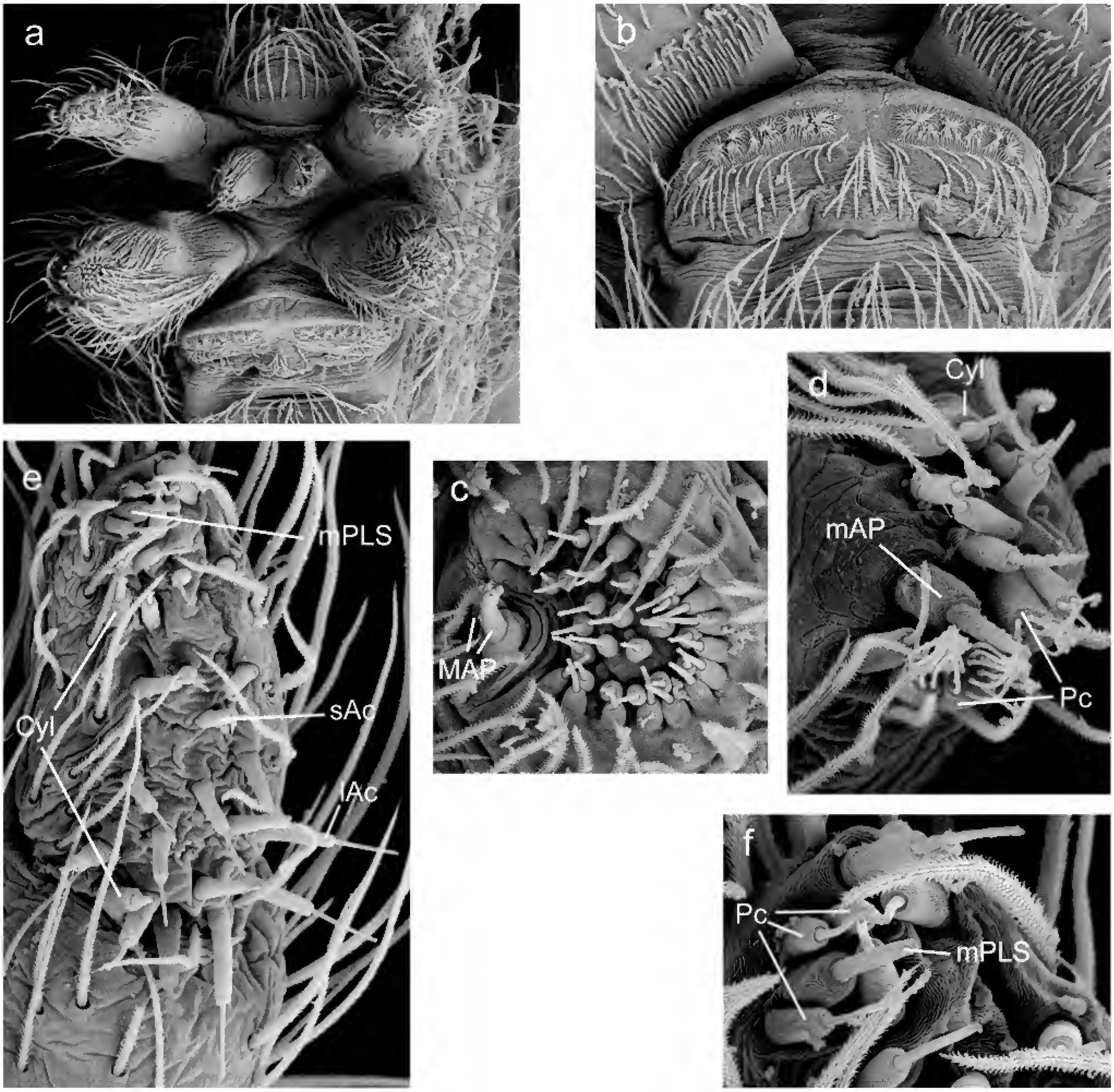

Fig. 9. *Pillara karuah* n.sp. (*a–f*) Spinnerets, female KS75399: (*a*) spinning field (cribellum below), (*b*) cribellum and spiracle. (*c–f*) Spigots: (*c*) ALS, (*d*) PMS, (*e*) PLS, (*f*) detail of PLS apex with modified PLS spigot. (Spigot abbreviations, see Fig. 3).

Female (KS70335). BL 6.49, CL 2.69 (2.04–2.73), CW 1.88, CapW 1.22, EGW 0.82, LL 0.41, LW 0.41, SL 1.29, SW 1.16. Legs: 1423 (I: 11.67; II: 9.42; III: 7.92; IV: 9.58); ratio tibia I length:CW = 1:0.63. Epigynum: (KS70337, Fig. 10c,d). Fossa a subcircular pit, copulatory ducts opening from anterior end, cuticular area anterior to fossa lip strongly sclerotized. Internal genitalia: (KS70337, Fig. 10e). Copulatory ducts moderately broad; spermathecae touching medially.

Variation. MA always reduced but varies from 1–2 membraneous "spines" to indistinct. The low, collar-like ridge around the MA base may be homologous with the fleshy part of the MA in *Borrala* spp.

Distribution. Barrington massif region, New South Wales.

Pillara macleayensis n.sp.

Figs. 8b, 11a–d

Etymology. The species name is taken from the Macleay River region which encompasses the type locality.

Types. **Australia, New South Wales**. HOLOTYPE ♂ KS34508, 3 mi E of Carrai on Kempsey road, 30°57'15"S 152°23'27"E, 26 Apr 1974, M.R. Gray. PARATYPES ♀ KS70130, data as holotype; ♂ KS34507, ♀ KS70131, Carrai, near top of Bat Cave Trail, 30°59'03"S 152°20'27"E, 26 Apr 1974, M.R. Gray, sheet web in litter; ♀ KS34764, Carrai Bat Cave, 30°58'59"S 152°19'49"E, under rock.

Other material. **Australia, New South Wales**. ♀ KS9419, Bellangry SF, Wilson River Flora Reserve, 31°18'S 152°29'E, 6 Mar 1981, M.R. Gray.

Diagnosis. Differs from other species in having the bifurcate RTA processes markedly dissimilar and widely divergent. Epigynal fossa very small.

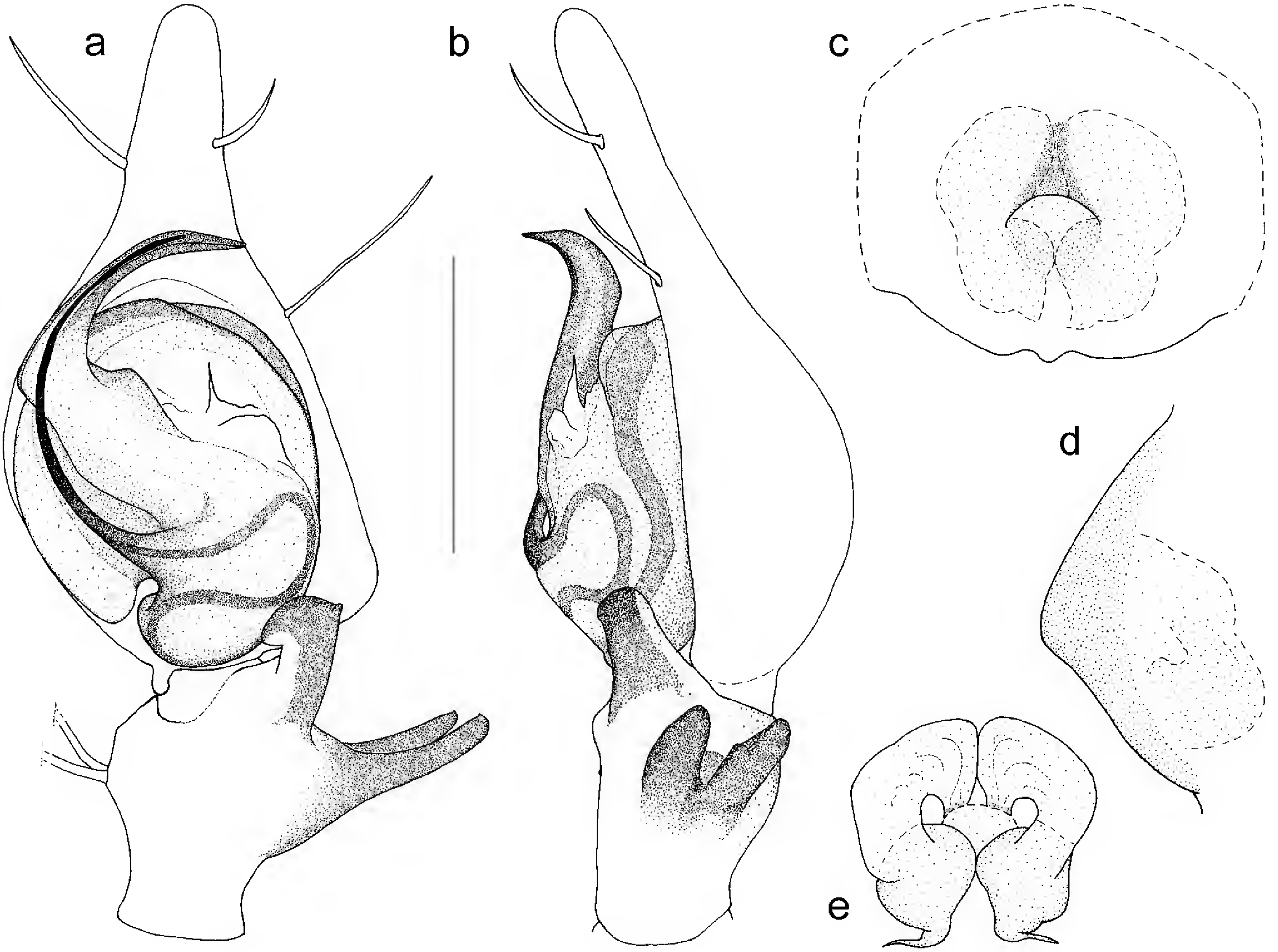

Fig. 10. *Pillara karuah* n.sp. (*a,b*) Male palp (KS34509): (*a*) ventral, (*b*) retrolateral. (*c–e*) Female epigynum (KS70337): (*c*) ventral, (*d*) lateral, (*e*) dorsal-internal genitalia. Scale line 0.5 mm.

Male (holotype). BL 5.96, CL 2.90 (2.73–2.90), CW 2.00, CapW 1.10, EGW 0.82, LL 0.39, LW 0.41, SL 1.39, SW 1.29. Legs: 1243 (I: 17.00; II: 14.25; III: 11.83; IV: 14.00); ratio tibia I length:CW = 1:0.37. Male Palp: (Fig. 11a,b). Deeply bifurcate RTA with large, thin, widely divergent and dissimilar processes, (ventral process long, tapering; dorsal process shorter, plate-like). RVTA with a small, acute retroapical ridge. Cymbial bristles weak. Tegular lobe basal. Embolic origin probasal. Conductor stalked, bent and extended retrolaterally as a sickle-like, grooved spine. MA a prominent, curved, membraneous process.

Female (KS70130). BL 5.96, CL 2.53 (2.37–2.53), CW 1.67, CapW 1.18, EGW 0.78, LL 0.35, LW 0.39, SL 1.22, SW 1.12. Legs: 1423 (I: 11.00; II: 8.92; III: 7.58; IV: 9.25); ratio tibia I length:CW = 1:0.59. Epigynum: (KS34764, Fig. 11c). Fossa a small pit set in a shallow broad depression; pit narrowest anteriorly where there is a small darker area of strongly sclerotized cuticle; copulatory ducts opening anterolaterally from fossa. Internal genitalia: (KS34764, Fig. 11d). Copulatory ducts less broad than in *P. karuah*; spermathecae closely adjacent medially.

Distribution. Carrai Plateau and the Hastings Range of New South Wales.

Pillara coolahensis n.sp.

Figs. 8b, 12a–d

Etymology. The species name is taken from the type locality.

Types. **Australia, New South Wales**. HOLOTYPE ♂ KS75016, Coolah Tops NP, Breeza Lookout, 31°49'17"S 150°11'28"E, 7 Nov 2001, M. Gray, G. Milledge & H. Smith, fine sheet webs with retreats in earth banks and rotting logs. PARATYPES: ♀ KS75023, data as holotype; ♂♂ KS75017–9, KS75386, KS75402, ♀♀ KS75020–22, data as holotype; ♀♀ KS75024–5, ♀♀ KS75387, KS77103, ♂ KS77104, Coolah Tops NP, Grass Tree Track, 31°44'06"S 150°00'05"E, 8 Nov 2001, M. Gray, G. Milledge & H. Smith, fine sheet webs with retreats in rotting logs; ♂, KS75400, ♀ KS75401, Coolah Tops NP, Bald Hill Track, 2.5 km from The Forest Rd, 31°45'S 150°01'E, 8 Nov 2001, M. Gray, G. Milledge & H. Smith, sheet webs, ♀ with eggsac.

Other material. **Australia, New South Wales**. ♀ KS75399, Coolah Tops NP, Grass Tree Track, data as KS75024, abdomen used for SEM.

Diagnosis. Large T-shaped conductor; tegular lobe and embolus origin retrolateral. Epigynum and fossa deeply sclerotized, fossa circular.

Male (holotype). BL 6.41, CL 3.06 (2.73–3.67), CW 2.24, CapW 1.39, EGW 0.82, LL 0.45, LW 0.46, SL 1.51, SW 1.37. Legs: 1423 (I: 15.25; II: 12.67; III: 9.75; IV: 12.83); ratio tibia I length:CW = 1:0.57. Male Palp: (Fig. 12a,b). Cymbium with well-developed retrolateral flange. Ventral

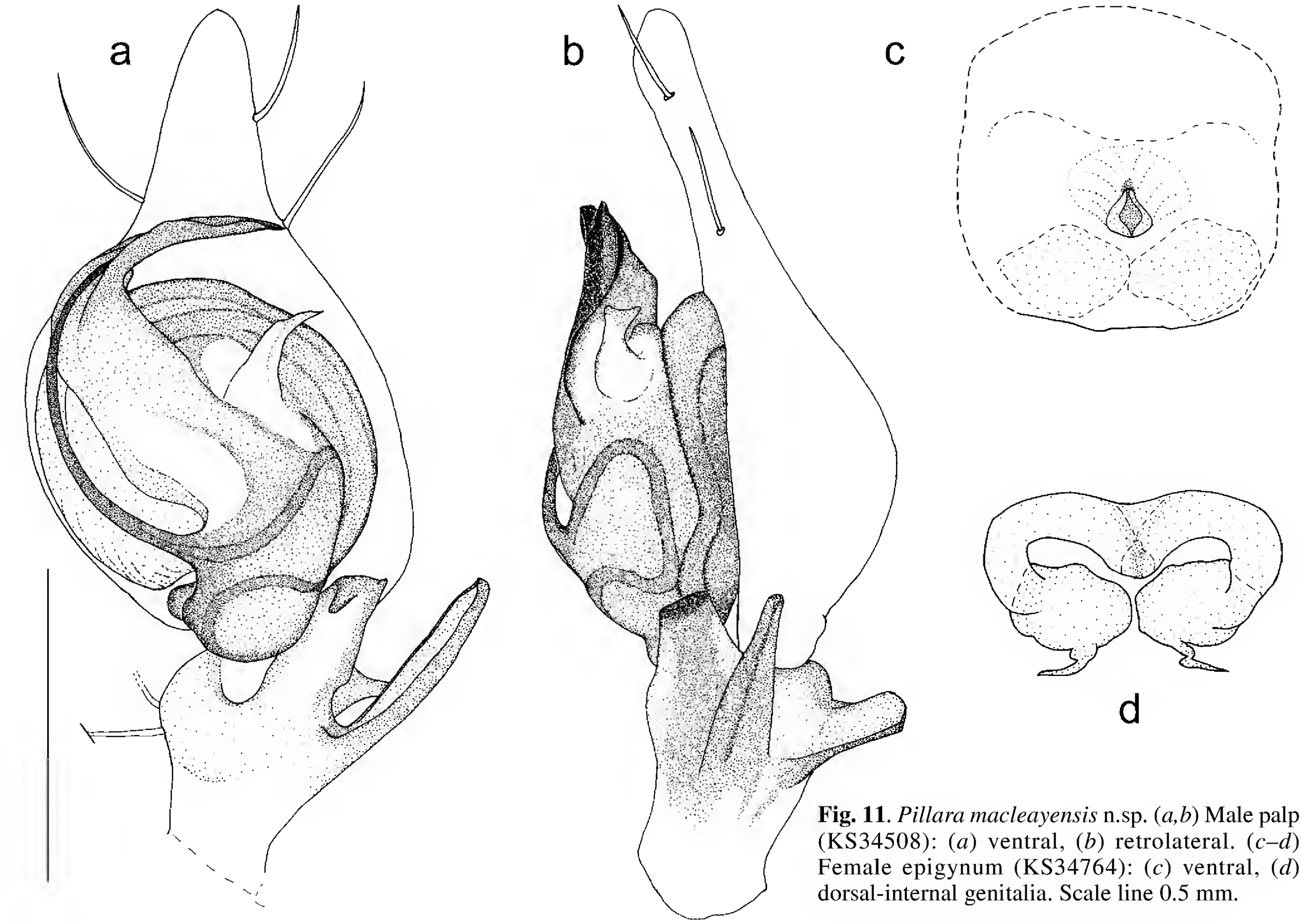

Fig. 11. *Pillara macleayensis* n.sp. (*a,b*) Male palp (KS34508): (*a*) ventral, (*b*) retrolateral. (*c–d*) Female epigynum (KS34764): (*c*) ventral, (*d*) dorsal-internal genitalia. Scale line 0.5 mm.

process of RTA larger and set higher than curved dorsal process, angled at about 45° to each other. RVTA slender with a prominent retroapical tubercle which projects into the relatively wide gap between the tegular lobe and the subtegulum. Bulb wider than long. Tegular lobe placed retrolaterally, distally truncate, with the tightly looped part of sperm duct contained largely within the lobe. Conductor a large, weakly sclerotized to membraneous T-shaped fan, with stronger sclerotization confined mainly to a corrugated lamina on the retrodorsal side of conductor stalk and the spine-like, ventrally curved, distal part of the conductor. Embolus long, strongly curved, origin retrolateral. Tegular window large, probasally placed. MA a thin, curved rod, distally sclerotized.

Female (KS75023). BL 8.58, CL 3.42 (2.45–3.35), CW 2.24, CapW 1.59, EGW 1.02, LL 0.53, LW 0.51, SL 1.63, SW 1.43. Legs: 1423 (I: 13.25; II: 10.67; III: 9.25; IV: 11.33); ratio tibia I length:CW = 1:0.65. Epigynum: (Fig. 12c). Fossa a sclerotized, circular pit with posterior groove, sometimes flanked by two small "dimples". Internal genitalia (KS75025, Fig. 12d). Copulatory ducts broad, with wide openings along lateral fossa; spermathecae large, in broad contact medially.

Distribution. Known only from Coolah Tops NP, NSW.

Comments. The unique position of the palpal bulb in this species was at first thought to be due to torsion of the bulb during preservation. However, all males examined show the same bulb orientation, which also correlates with the T- shaped expansion of the conductor and the elongate embolus.

Pillara griswoldi n.sp.

Figs. 8b, 13a–e

Etymology. The species is named in honour of Charles Griswold, Californian Academy of Sciences, one of the collectors.

Types. **Australia, New South Wales**. HOLOTYPE ♂ KS72857, Gloucester River camp ground, Barrington Tops NP, 32°04'S 151°41'E, webs on/under mossy logs, M.R. Gray & H.M. Smith, 22 Nov 1996. PARATYPES: ♀ KS72858, ♂♂ KS72859, KS72860, data as holotype; ♂, ♀ (CAS), locality data as holotype, 14 Aug 1990, C. Griswold; ♀ KS41330, Mountain Rd, 0.2 km S of junction with Kunungra Rd, 32°08'S 151°44'E, 4 Feb–9 Apr 1993, M. Gray & G. Cassis, NE NSW NPWS Survey; ♂♂ NN19551–2 (SAM), O'Sullivans Gap, Bulahdelah SF, 32°19'S 152°16'E, under log, 14 May 1988, D. Hirst.

Diagnosis. Separated from all other species by presence of long, rod-like, mid-retrolateral process on RVTA and large, sclerotized, anteromedial knob on epigynum.

Male (holotype). BL 5.27, CL 2.62 (2.53–2.62), CW 1.89, CapW 1.11, EGW 0.77, LL 0.42, LW 0.43, SL 1.44, SW 1.21. Legs: 1243 (I: 15.16; II: 12.51; III: 10.25; IV: 12.47); ratio tibia I length:CW = 1:0.47. Male Palp: (Fig. 13a,b). Bifurcate RTA processes robust, apically pointed, relatively shorter than in other species, subparallel to weakly angled; subapical spine present on thicker dorsal process. RVTA relatively short, and with a long, mid-retrolateral, rod-like process. Tegular lobe basal. Conductor a short wide stalk, widely bifurcate distally with two pointed processes, ventral process spine-like and sclerotized, dorsal process triangular

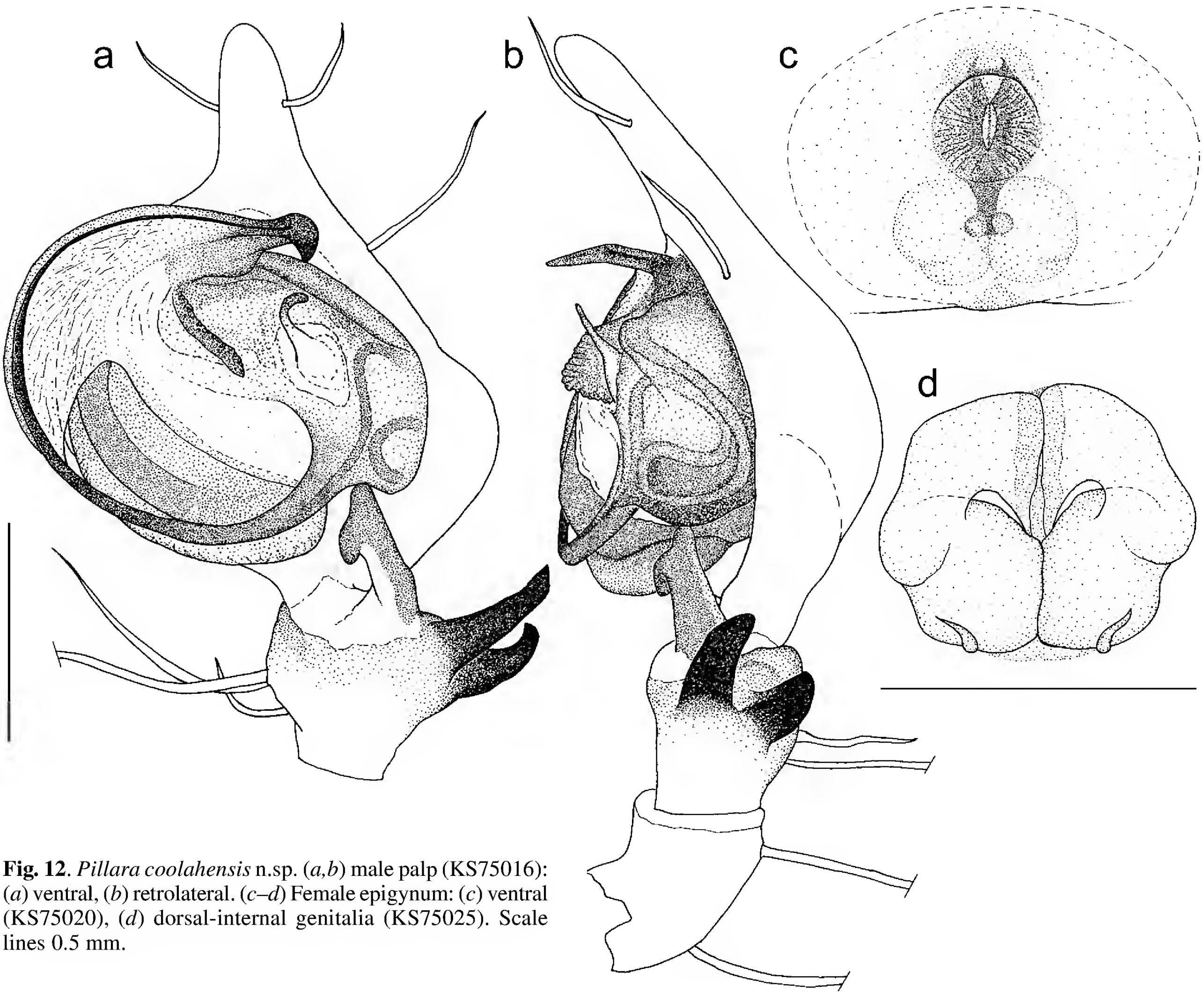

Fig. 12. *Pillara coolahensis* n.sp. (*a,b*) male palp (KS75016): (*a*) ventral, (*b*) retrolateral. (*c–d*) Female epigynum: (*c*) ventral (KS75020), (*d*) dorsal-internal genitalia (KS75025). Scale lines 0.5 mm.

and membraneous. Embolus relatively short, running from probasal origin into groove on ventral conductor process. MA reduced to a fleshy process. Tegular window very small.

Female (KS 72858). BL 5.78, CL 2.33 (2.24–2.41), CW 1.45, CapW 0.98, EGW 0.70, LL 0.36, LW 0.32, SL 1.14, SW 1.01. Legs: 1423 (I: 10.07; II: 7.53; III: 5.78; IV: 8.07); ratio tibia I length:CW = 1:0.56. Epigynum: (Fig. 13c,d). Epigynal fossa absent. Large, sclerotized, knob-like apophysis placed on anteromedial epigynum and flanked on each side by a lateral groove and ridge converging posteriorly; long copulatory grooves open lateral to each ridge. Internal genitalia: (Fig. 13e). Very short copulatory ducts lead from the copulatory grooves into ovoid spermathecae that are in broad contact medially.

Distribution. Eastern Barrington massif to the Bulahdelah area of NSW.

Comments. This is the most derived representative of the genus in both male palpal and epigynal characteristics. The epigynal structure is especially altered from the general generic pattern. The development of the massive anterior apophysis on the epigynum appears to have obliterated the pit-like fossa and pushed the copulatory duct openings laterally and ventrally to a surface position.

Discussion

***Borrala* and *Pillara* characters**. There are several marked structural trends and differences in the genitalia. Both genera have large palpal tibial apophyses, with a stalked, "crochet hook" RVTA, a broad tegular lobe especially prominent in *Pillara*, a moderate–small tegular window and a variably T-shaped to stalked conductor. In *Pillara*, the RTA is deeply bifurcate with two robust processes. The MA is unipartite (although remnants of a bipartite state may be present in *P. karuah*), usually non-sclerotized and often reduced. In *Borrala*, the RTA is undivided and apically spine-like. The MA is unusual in having a bipartite structure, consisting of a ventral non-sclerotized process and a dorsal sclerotized process. This character may link *Borrala* with other "striped" group genera (Gray & Smith, in prep.) with bipartite MA that range through forested areas from Papua New Guinea to southwestern Australia.

Both *Borrala* and *Pillara* species typically have moderately sclerotized epigyna with unpaired pit-like fossae, placed anterior to the paired spermathecae. In *Borrala*, the fossa is longer than wide, narrower anteriorly or ovoid. In *Pillara*, the fossa is more rounded, often with a deeply sclerotized area of cuticle in front of the anterior margin where the fossa lip and the medial walls of the copulatory ducts meet. However, in one highly derived

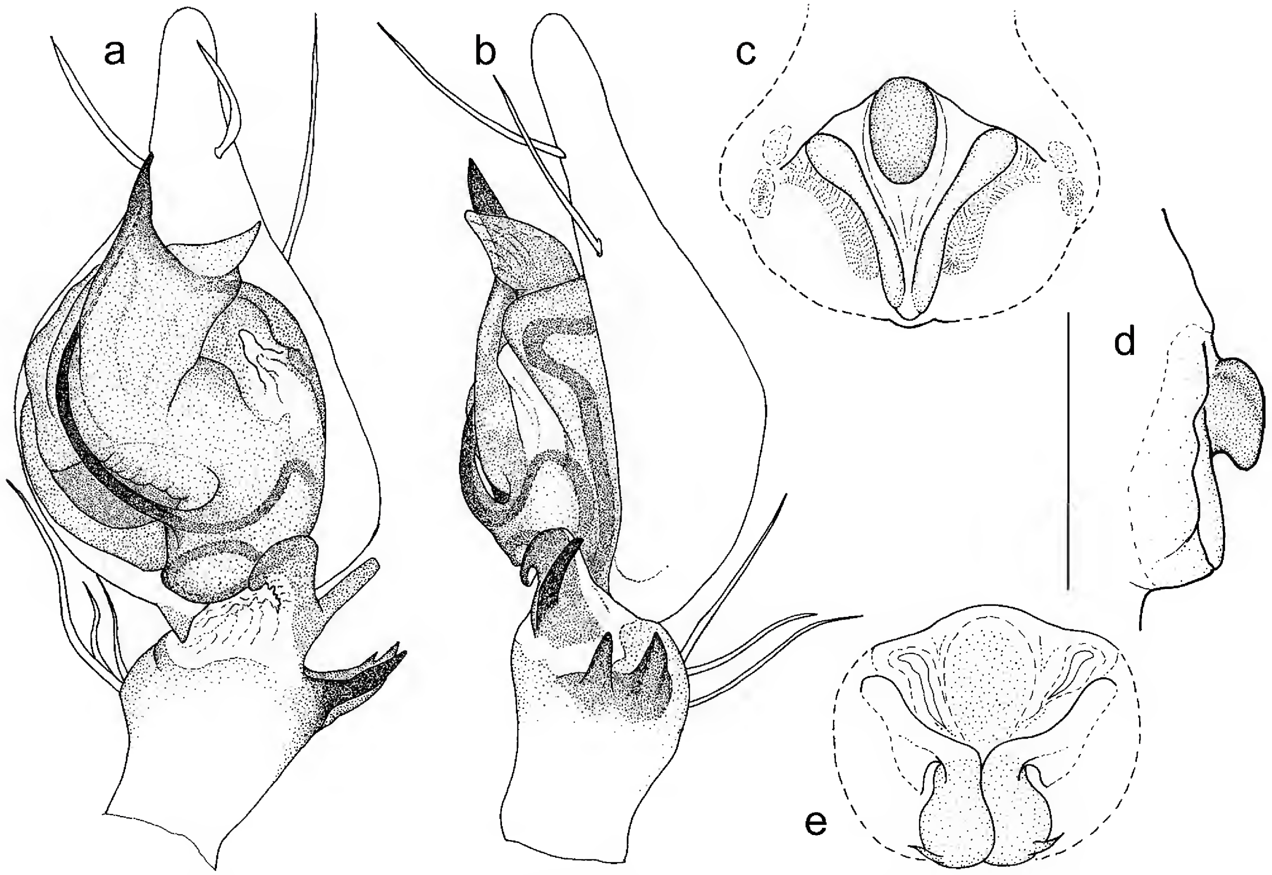

Fig. 13. *Pillara griswoldi* n.sp. (*a,b*) Male palp (CAS): (*a*) ventral, (*b*) retrolateral. (*c–d*) Female epigynum (*c*) ventral (KS72858), (*d*) lateral (CAS), (*e*) dorsal-internal genitalia (KS72858). Scale line 0.5 mm.

species (*P. griswoldi*) this area is hypertrophied into a sclerotized, knob-like apophysis.

Comments on relationships. *Therlinya* (Gray & Smith, 2002) and the "striped" group of genera described here (and in Gray & Smith, in prep.) share the presence of a well-defined tegular lobe, a uni- or bi-partite MA (both parts, or at least one, membraneous), and grate-shaped tapeta in the posterior eyes. However, both the longitudinally striped patterning of the carapace and its dorsal profile (highest at the fovea), as well as the larger eyes, differentiate the genera described here from both *Therlinya* and the *Taurongia* group genera (Gray & Smith, 2002). At least among these groups, these character states may be derived for the "striped" group, although all appear elsewhere in the Amaurobioidea. The presence of a similar carapace profile and longitudinal stripes in some Kababininae (Davies, 1999), which is associated with *Stiphidion* in Davies & Lambkin (2000), is of particular interest.

The eye tapetum structure in these genera is of particular interest. Contrary to Homann (1971), followed by Griswold *et al*. (1999) and Gray & Smith (2002), the eyes of *Stiphidion* (*S. facetum* ex Hornsby, NSW) lack grate-shaped tapeta; canoe-shaped tapeta are present in the ALE but no tapeta are discernible in the posterior eyes. The presence of a grate-shaped tapetum clearly is not a defining feature of *Stiphidion* or the Stiphidiidae. However, putative stiphidiids like *Therlinya* and the "striped" genera described here all possess grate-shaped tapeta in the PLE and PME (with canoe-shaped tapeta in the ALE). The distribution of the various tapetum types is proving useful in establishing relationships between putative "stiphidiid" genera and potentially for other groupings within the Amaurobioidea.

ACKNOWLEDGMENTS. This project received funding assistance through the New South Wales Biodiversity Strategy: Taxonomy Enhancement Research Grants. We thank Dr Charles Griswold of the Californian Academy of Sciences and Mr D. Hirst of the South Australian Museum for the loan of material.

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